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# THE LEAF ARCHITECTURE OF *TICODENDRON* AND THE APPLICATION OF FOLIAR CHARACTERS IN DISCERNING ITS RELATIONSHIPS<sup>1</sup>

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## ABSTRACT

Leaves of the recently described genus *Ticodendron* are simple, alternate, stipulate, symmetrical, elliptical with attenuate apices and acute bases, a single order of serrations representing modified rosid teeth, pinnate, craspedodromous principal venation, percurrent tertiaries, well-developed, random areolation, anomocytic stomates, and T-shaped hairs. Phenetic and cladistic analyses of leaf and other characters of *Ticodendron* were performed in order to determine its affinities and evolutionary relationships. Several new characters, including the number of veins joining the midrib and the venation of the marginal teeth, were added to the suite of standard leaf architectural descriptors because of their demonstrated potential as systematic indicators. After filtering out nonapplicable and symplesiomorphous characters, a total of 70 characters (48 leaf and 22 reproductive and wood) remained. These were organized into two main data sets, with the second further divided to form three subsets, which were then analyzed using a simple similarity comparison and parsimony methods. From the standpoint of its gross phenetic and phylogenetic affinities, *Ticodendron* belongs to a group of amentiferous taxa, with the extinct genus *Fagopsis* showing the strongest affinity, followed by *Brunellia*, *Castanopsis*, *Castanea*, *Alnus*, and *Nothofagus*. Our cladistic analyses show *Ticodendron* grouping with the Fagales and occasionally with the Myricaceae in a rosalean clade whose base is embedded in the Cunoniaceae. These data support recognition of the new genus as a member of a distinct family in the order Fagales and with closest affinities to Fagaceae and Betulaceae.

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The recent discovery of a relatively common tree of unknown affinities in middle elevation, wet primary forests of Panama and Costa Rica is vivid evidence of what is being lost as the deforestation of the tropics continues.

Determining the systematic affinities of *Ticodendron* Gómez-Laurito & Gómez P. is especially challenging because it has a mosaic of characters that defy ready placement. Its general affinity is with the more derived members of the highly unnatural group of dicotyledons with reduced flowers (Behnke, 1989; Thorne, 1989; Wolfe, 1989) known as the Amentiferae. Thus, during the exchanges by the working group, evidence has been cited for relationships to families as disparate as the Euphorbiaceae, Dilleniaceae, Juglandaceae, Betulaceae, and Ulmaceae. However, detailed anatomical and morphological investigations by members of the group are beginning to provide reliable characters. A consensus has developed that the affinities of

*Ticodendron* lie near a group of amentiferous families that comprise the Hamamelidae of Cronquist and that include the Fagaceae, Betulaceae, Myricaceae, and possibly Juglandaceae.

The main objectives of this paper are to provide a concise and rigorous description of the leaves of *Ticodendron* and an assessment of its affinities, with an emphasis on foliar characters. We will also examine its phylogenetic relationships based on leaf and other characters assisted by cladistic techniques. Throughout, we will attempt to show the concordance between inferences of relationship that arise from an analysis of leaf characters with those of other organs. Our focus on leaves is based on the fact that they are morphologically complex organs, with a diversity of characters such as teeth and detailed venation patterns that often indicate phylogenetic affinity (Hickey & Wolfe, 1975). However, precisely because it now appears that certain elements of leaf architecture are congruent

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with systematic affinity at higher taxonomic levels, it is essential that more rigorous and explicit techniques of phylogenetic analysis be applied to lower taxonomic levels of the angiosperms in order to demonstrate the utility of leaf characters.

A number of such test cases already exist or are being developed. Levin (1986a, b, c) explicitly studied the correlation between the relationships based on leaf characters with phylogenies based on traditional characters within the Euphorbiaceae, a notoriously difficult family. The phenetic and cladistic results not only show the similarity between leaf and other data sets, but also suggest that the leaf data may be superior in some cases. Levin now plans to extend this survey to the Flacourtiaceae (pers. comm.). More recently, Todzia & Keating (in press) used foliar characters to distinguish clades in the Chloranthaceae where reproductive characters had provided ambiguous results. So has Hershkovitz (1988), who reported that such leaf architectural characters as vein course and leaf rank prove useful in the systematic interpretation of the Centrospermae, a group whose predominantly herbaceous character might lead to an inference of a high degree of leaf architectural plasticity and attendant homoplasy. Finally, Miller & Nowicke (1990) have used leaf architectural characters, in conjunction with a suite of other characters, to show the relationships of two genera in Boraginaceae.

At the present time, this and other evidence suggest that leaves may well provide information on phylogenetic relationships that is at least equal to that derived from any other organ or data set in the plant. Thus, although the major purpose of this study is to describe and elucidate the relationships of *Ticodendron*, we also hope to show that cladograms based on leaf characters are similar to those derived from other organs. To optimize our use of leaf characters, we refined and extended many of their definitions, such as tooth type, so that they would be more useful in distinguishing entities and in pointing to relationships at lower taxonomic levels. This increased the general robustness and utility of our leaf characters as well as elucidated the relationships of *Ticodendron* itself.

#### MATERIALS AND METHODS

Cleared leaves of *Ticodendron* were prepared for this study from two specimens supplied by MO. These were prepared by the methods outlined in Hickey (1979) and Hickey & Wolfe (1975). Comparisons were made using the cleared leaves found

in the National Cleared Leaf Collection (NCLC) housed at Yale Peabody Museum (YPM). Additional vegetative characters as well as the reproductive characters used were obtained by study of herbarium specimens housed at YU and NY or by recourse to the literature of systematic and comparative botany. A list of taxa examined, both from cleared leaves and herbarium specimens, appears in Table 1.

After a broad search of the National Cleared Leaf Collection at Yale University, 18 operational taxonomic units (OTUs) at the generic level from eight families (Table 1) were selected for detailed comparison to *Ticodendron*. This group included representatives from five amentiferous families, namely species of *Castanea*, *Castanopsis*, *Nothofagus*, the extinct genus *Fagopsis* (Fagaceae), *Alnus* (Betulaceae), *Pterocarya*, *Platycarya* (Juglandaceae), *Canacomyrica*, *Myrica* (Myricaceae), and *Rhoiptelea* (Rhoipteleaceae). In addition, several clades from three putatively primitive families of Rosales were examined. These included *Brunellia* (Brunelliaceae); *Davidsonia* (Davidsoniaceae); and *Acsmithia*, *Ceratopetalum*, and *Cunonia* (as representatives of Cunoniaceae). The genera of Cunoniaceae were chosen due to their apparently primitive phylogenetic position within the family based on leaf, reproductive, and wood characters (Dickison, 1980b) and general similarity to *Ticodendron*.

Formulation of a list of characters and character states that adequately described the leaf architecture of *Ticodendron* and allowed its comparison with other taxa was a crucial aspect of this analysis. Our starting point was the outline of leaf architectural characters established by Hickey (1979). As we collected data we found other overlooked characters that proved to have potential value in determining relationships. This led to an expansion in the terminological base, especially for characters that deal with tooth morphology and marginal venation (see Results below).

Initially, 71 vegetative characters were collected from cleared leaves and herbarium specimens. These included leaf architectural as well as node, stipule, cuticular, and twig features. In addition, seven wood characters and 17 floral and pollen characters were obtained from the working group and the literature (Gómez-Laurito & Gómez P., 1989; Carlquist, 1991; Feuer, 1991; Tobe, 1991). The high degree of similarity that characterizes the pollen of many of these OTUs (Batten, 1989) has been suggested to be a shared derived character for some groups of families in the Hamamelidae (Muller, 1984).

TABLE 1. List of species, OTU abbreviation, and collection information for the specimens used to generate the leaf architectural and other vegetational data used in this study. Fossil collections: YPM—Yale Peabody Catalogue for Fossil Plants; YPM-PU—Peabody Coll. ex Princeton Univ. Paleobotanical Coll.

Genus (family)	OTU	Source of leaf architectural characters	Source of other vegetative characters
<i>Ticodendron</i> (unknown)	TICO	<i>T. incognitum</i> (Hammel, Bello, Haber, Kinsman & Lierheimer 15285, YU), (NCLC 6383) <i>T. incognitum</i> (McPherson 8401, YU ex MO), (NCLC 6765)	same
<i>Fagopsis</i> (fossil) (Fagaceae)	FAGO	<i>F. longifolia</i> YPM 25404, 25467; YPM-PU 9809	same
<i>Brunellia</i> (Brunelliaceae)	BRUN	<i>B. colombiana</i> (Cuatrecasas & Llano 27314, US), (NCLC 3186) <i>B. racemifera</i> (Barclay et al. 3413, US), (NCLC 3190)	<i>B. comocladifolia</i> (Wright 1133, YU)
<i>Acsmithia</i> (Cunoniaceae)	ACSM	<i>A. densiflora</i> (Hickey 5274, YU), (NCLC 6545)	same
<i>Ceratopetalum</i> (Cunoniaceae)	CERA	<i>C. gummiferum</i> (Wilkes s.n., YU), (NCLC 6713)	same
<i>Cunonia</i> (Cunoniaceae)	CUNO	<i>C. capensis</i> (Cummings 300, US), (NCLC 3165)	<i>C. cf. deplanchei</i> (Hickey 5252, YU)
<i>Davidsonia</i> (Davidsoniaceae)	DAVI	<i>D. puriens</i> (Cronquist 11622, NY), (NCLC 6766)	
<i>Pterocarya</i> (Juglandaceae)	PTER	<i>P. stenocarpa</i> (Hickey s.n., YU), (NCLC 3220)	<i>P. caucasia</i> (Brewer s.n., YU)
<i>Platycarya</i> (Juglandaceae)	PLAT	<i>P. strobilacea</i> (Chen 3706, GH), (NCLC 7001) <i>P. strobilacea</i> (1757053, US), (NCLC 410)	<i>Englehardtia spicata</i> (Merrill 253, YU)
<i>Rhoiptelea</i> (Rhoipteleaceae)	RHOI	<i>R. chiliantha</i> (1577640, US), (NCLC 804)	none
<i>Canacomyrica</i> (Myricaceae)	CANA	<i>C. monticola</i> (Hickey 5210, YU), (NCLC 6768)	same
<i>Myrica</i> (Myricaceae)	MYRI	<i>M. cerifera</i> (358864, US), (NCLC 143) <i>M. californica</i> (E. Hall 468, YU), (NCLC 6781)	<i>M. cerifera</i> (Curtiss 2606, YU)
<i>Castanopsis</i> (Fagaceae)	CAOP	<i>C. concolor</i> (Schoh 101, US), (NCLC 627)	<i>C. chrysophylla</i> (E.W. Hammond 346, YU)
<i>Castanea</i> (Fagaceae)	CAST	<i>C. pumila</i> (Kearney, Jr. 892, US), (NCLC 6136)	<i>C. dentata</i> (Godfrey s.n., YU)
<i>Nothofagus</i> (Fagaceae)	NOH1	<i>N. discoidea</i> (Baumann-Bodenheim 15111, US), (NCLC 221)	<i>N. balansea</i> (Hickey s.n., YU)
<i>Nothofagus</i> (Fagaceae)	NOH2	<i>N. fusca</i> (Walker 4696, US), (NCLC 1765) <i>N. moorei</i> (ex Herb. Melbourne s.n., US), (NCLC 55)	<i>N. balansea</i> (Hickey s.n., YU)
<i>Alnus</i> (Betulaceae)	ALN1	<i>A. nepalensis</i> (Stibolt s.n., US), (NCLC 5387)	<i>A. crispa</i> (A. Hill 2541, YU)
<i>Alnus</i> (Betulaceae)	ALN2	<i>A. rhombifolia</i> (Plaskett s.n., US), (NCLC 5402)	<i>A. crispa</i> (A. Hill 2541, YU)

Several operational difficulties were encountered in coding the tooth characters. Problems included the existence of two different types of teeth (cunonioid and rosid; Hickey & Wolfe, 1975) on the same leaf, and in rare cases transitional forms, both in the same species and in closely related taxa, that lay morphologically between the common

basic teeth types (e.g., in Juglandaceae, *Rhoiptelea*, *Davidsonia*, and Myricaceae).

Each tooth type can be described by a suite of characters (see below, Fig. 2). To describe two tooth types in a single taxon, it is necessary to have two sets of descriptive tooth characters, one for each type. Thus tooth type 1 (cunonioid) is

coded by characters 6–11 and type 2 (rosid) by characters 12–17 and 20. This created a problem when an OTU had only one tooth type. Normally, if a character is missing, it is either coded as unknown, which allows computerized cladistic algorithms to assign an optimal state, or coded as a single character state for the absence of the character. Yet if an entire tooth is missing, in the second case each state of the entire suite of characters is coded as absent, and these states could act as shared derived characters for a group of taxa. Yet the absence of these characters could be due to parallel loss, the ancestral condition (thus are symplesiomorphies), or actual shared derived states. This presents difficulties for our analysis because the lack of rosid teeth is also ancestral, based on outgroup comparison. Our solution was to code each of the characters of the missing tooth type as a nonapplicable state (NA) in the cases where only one tooth type existed. We created an NA state for each family where at least one OTU was lacking a tooth type. We suggest that this method results in underweighting of these characters (they are either autapomorphies or synapomorphies at the top of the tree), but at least avoids grouping taxa based on symplesiomorphies or on less secure character loss states.

In order for our analysis to deal with OTUs having transitional teeth, we chose to use the most fully developed extreme of each of the two tooth types. In fact, in a given OTU these extremes tended to be the most common.

Once the matrix was formed, we found a number of characters, particularly of the leaf, that proved to be inappropriate at the level we were using them. They were removed if they either did not vary at the taxonomic level being examined or if they were polymorphic at the generic level and thus only useful for elucidating specific relationships. In addition, we removed all autapomorphic characters, characters in which many of the OTUs were missing data, and finally, a few characters that further study indicated were not structurally homologous.

The remaining 70 characters (48 leaf and 22 reproductive and wood) were used in our phylogenetic analysis (Appendix). Some OTUs had multiple character states for specific characters (the states not used in the analysis are provided at the end of the description of each character in the Appendix). Since the version of PAUP we used to implement our cladistic analysis can only use one state for each OTU, we had to devise an objective protocol in order to decide which character states to include for a given OTU. For an OTU, if a character was polymorphic and shared a state with

*Ticodendron*, we chose that state because the principal objective of this analysis was to ascertain the affinities of *Ticodendron*. If none of the states were the same as those of *Ticodendron*, the state that was most common in the OTU was chosen. If all states were equally common, the state most common for all of the OTUs was used. If none of the states were similar to the most common state, we used the state most similar to that of a closely related taxon. Finally, if two closely related taxa (same family or genus) shared two character states, each OTU was assigned a different state.

The resulting data matrix was arranged to form two sets (Tables 2, 3), with the second set divided into two additional subsets (characters 1–48 and 49–70). The first set (Table 2) included all 18 OTUs and the vegetative characters, excluding wood (characters 1–48). To compare vegetative and other data sets it was necessary to reduce the number of OTUs because data on reproductive and wood morphology were missing for several of the OTUs, or were the same for *Nothofagus*2 and *Alnus*2. Thus, our second data set (Table 3) had 14 OTUs and 70 characters. Two types of analyses were performed on each of the two data sets. First was a simple similarity comparison, whose similarity coefficient was calculated by counting the number of character states shared by *Ticodendron* and each OTU and dividing it by the number of known characters. The remaining analyses were based on synapomorphy and parsimony. Our phylogenetic analysis used the program PAUP (Swofford, 1985). The major options of this program that we used were global branch swapping, mulpars, and rooting to a hypothetical ancestor to find the shortest trees. Variable options were ordering of the characters with two or rarely three character states, the option to treat the characters as completely unordered (those characters which are ordered are indicated as such in the Appendix), and the initial addition of sequence either closest or simple. Lastly, if multiple parsimonious trees were found, the trees were combined to form strict consensus trees (Swofford, 1985). The specific choice of outgroups, construction of the hypothetical ancestor, the method of ordering, and the resulting trees are discussed in the Results section below.

## RESULTS

In the following description of the leaves of *Ticodendron* and analysis of its affinities, the terms used are from Hickey (1979) with the addition of the following new terms or clarification of previous ones:

TABLE 2. Input data matrix for data set 1. OTUs are identified in Table 1 and characters are described in the Appendix.

OTU	Characters
	111111111222222222233333333334444444444 123456789012345678901234567890123456789012345678
1 HYPO	000
2 TICO	110212233343536352052110010111121103113021203311
3 FAGO	11010445457354452214211001?1112?111????21213304
4 BRUN	01020000000343635216211001??00220000110010103321
5 ACSM	1002110010100000000210000000010020?00000000010
6 CERA	000000025020000003000000000002101124100100003300
7 CUNO	000000025020000002100010010002020004?13000000000
8 DAVI	011301011003335351162100120113200200011000002200
9 PTER	011000010003336354161102220200121001112110012210
10 PLAT	011200000003336361162102220210220201112110000210
11 RHOI	011200000103436352162100110100110201104010000110
12 CANA	111100000103336350161102302302110001125100101100
13 MYRI	110400001003436460162102300301221001125220201100
14 CAOP	110015566683336352062200100011220001101221202312
15 CAST	110505566683336342060210100013220001101221003312
16 NOH1	110100100061221213022101001100221002111021010300
17 NOH2	111010001023436350152201001112221112101021213000
18 ALN1	111100001003335550131210010102211001102221000010
19 ALN2	111103342453343350141210010111211111102221213313

(1) *sinus*—an indentation in the margin of the leaf associated with a tooth or a lobe. Their identification is straightforward if they are angular, but shallow, rounded sinuses may grade imperceptibly into undulations of an entire margin. In such cases, sinuses may be recognized by measuring the maximum depth of the marginal indentation and comparing this with the distance to the apex of the

closest tooth (Fig. 1). This is done by dropping a perpendicular (cd in Fig. 1) to the nadir of the indentation from a line (ab) connecting the apices of the adjacent teeth and comparing the length of this line with the distance (in this case ac) to the closest tooth. If the depth (cd) is greater than the distance to the closest tooth (ac or bc) the marginal indentation is a sinus, otherwise not.

TABLE 3. Data matrix for data set 2. OTUs are identified in Table 1 and characters are described in the Appendix.

OTU	Characters
	11111111122222222223333333333444444444455555555566666666667 1234567890123456789012345678901234567890123456789012345678901234567890
1 HYPO	000
2 TICO	1102122333435363520521100101111211031130212033112141200001011212301111
3 FAGO	11010445457354452214211001?1112?111????2121330400500?????0111???011??
4 BRUN	01020000000343635216211001??00220000110010103210000002330?000003130200
5 ACSM	1002110010100000000210000000010020?0000000001000600000000000100200
6 CERA	0000000250200000030000000000021011241001000033000200020201000010030200
7 CUNO	000000025020000002100010010002020004?130000000002040000000001140020000
8 DAVI	011301011003335351162100120113200200011000002200100?222000120413120210
9 PTER	0110000100033363541611022202001210011121100122101141242101001351200211
10 PLAT	0112000000033363611621022202102202011121100002101141242101001351201211
11 RHOI	0112000001034363521621001101001102011040100001102141200000000113000210
12 MYRI	1104000010034364601621023003012210011252202011001141202001001151211211
13 CAST	110505566683336342060210100013220001101221003312003013101?000033020211
14 NOH1	110100100061221213022101001100221002111021010300211103301?0111?2401211
15 ALN1	111100001003335550131210010102211001102221000010214110102?011112401211

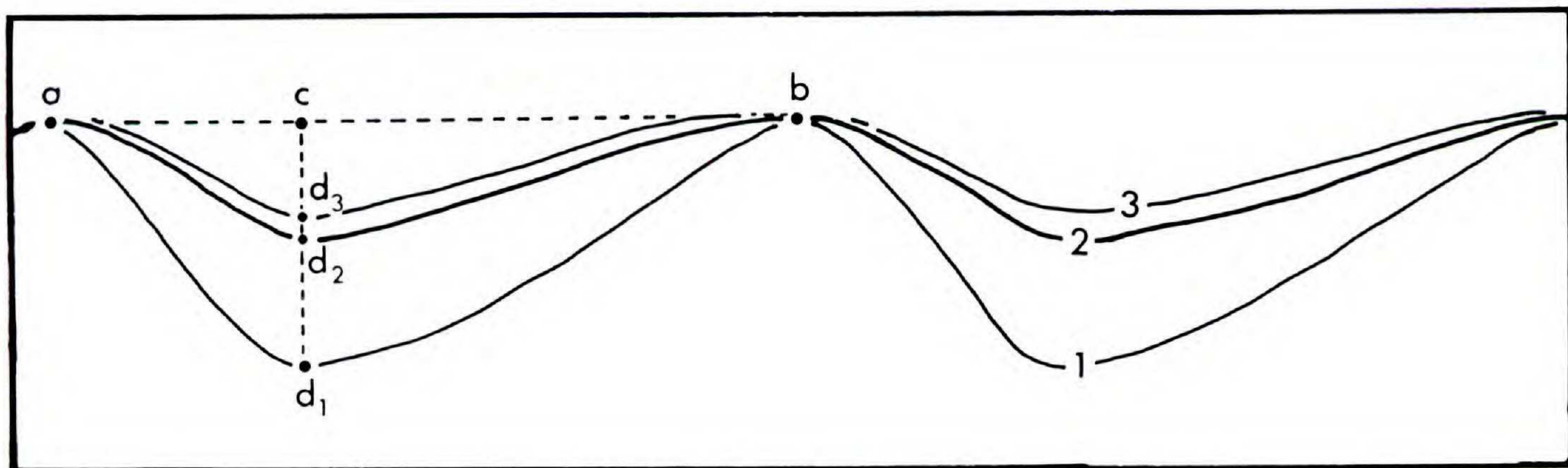


FIGURE 1. Determination of the presence of a sinus between teeth in three different marginal configurations (labeled 1, 2, and 3) where the nadir of the indentation is rounded. Tooth apices lie at points a and b, with d indicating the nadir of the sinus (in the case of  $d_1$ ) or of the marginal indentation ( $d_2$  and  $d_3$ ). Where  $cd > ac$  or  $cb$  the indentation is a sinus; where  $cd < ac$  or  $cb$  the indentation is not.

In the course of this work we found it necessary to elaborate upon the terminology available to describe the types of venation and vein courses at the margin and especially within the teeth of the leaf. The complete list of character states for these appear in the Appendix, but we give definitions for several of the most important characters below because of their importance in our analysis.

The first set of these are the veins associated with the teeth. These begin with:

(2) the *principal vein*—the thickest vein found within the confines of the tooth (Fig. 2, P). This is followed by:

(3) the *admedial vein*—the first branch from the principal vein below the tooth apex on the admedial side of the tooth (if from a tooth located at the leaf apex, then the first branch from either side of the principal vein that has the subsequent characters) that is the same, or one vein order lower than the principal vein, is distal to any exmedial vein of similar strength, and has  $> 60\%$  of its vascular tissue at its junction with the principal directed away from the tooth apex (Fig. 2, Ad).

(4) *accessory veins*—collectively, all the veins between the tooth apex and the admedial vein that either branch from or merge with the principal vein including the *conjunctal veins* (defined below) (Fig. 2, Ac).

(5) *conjunctal veins*—accessory veins of the tooth that converge upon or merge with the principal vein and contribute vascular tissue to the tooth apex. Conjunctal veins must have at least 60% of their vascular tissue directed toward the tooth apex at their point of convergence or fusion with the principal vein. They may occur in pairs, arising either oppositely or alternately to one another, or they may be single (Fig. 2, C).

(6) *comb vein*—an admedial branch of a secondary vein, arising near the margin and running along it, from which originate several tertiary veins that run admedially to the superadjacent secondary vein (Fig. 5, C). They occur singly or sometimes as an inner and an outer comb vein.

In an unpublished survey of angiosperm venation, we have noted that the number and configuration of the different classes of veins arising from the midvein of the leaf have proven to be of considerable value in determining affinity. Because the categories of veins used in this analysis carry an inference of evolutionary homology, we felt that a new set of terms was necessary to distinguish them from venation terms such as secondary, tertiary, and intersecondary in the system of Hickey (1979) where categories are recognized strictly on the basis of similarity in course and size where they attach to the midvein. These new terms are as follows:

(7) *deuteral veins*—consisting of the secondary veins of a leaf, the midveins of lateral leaflets, lateral primaries, and all those secondaries of the

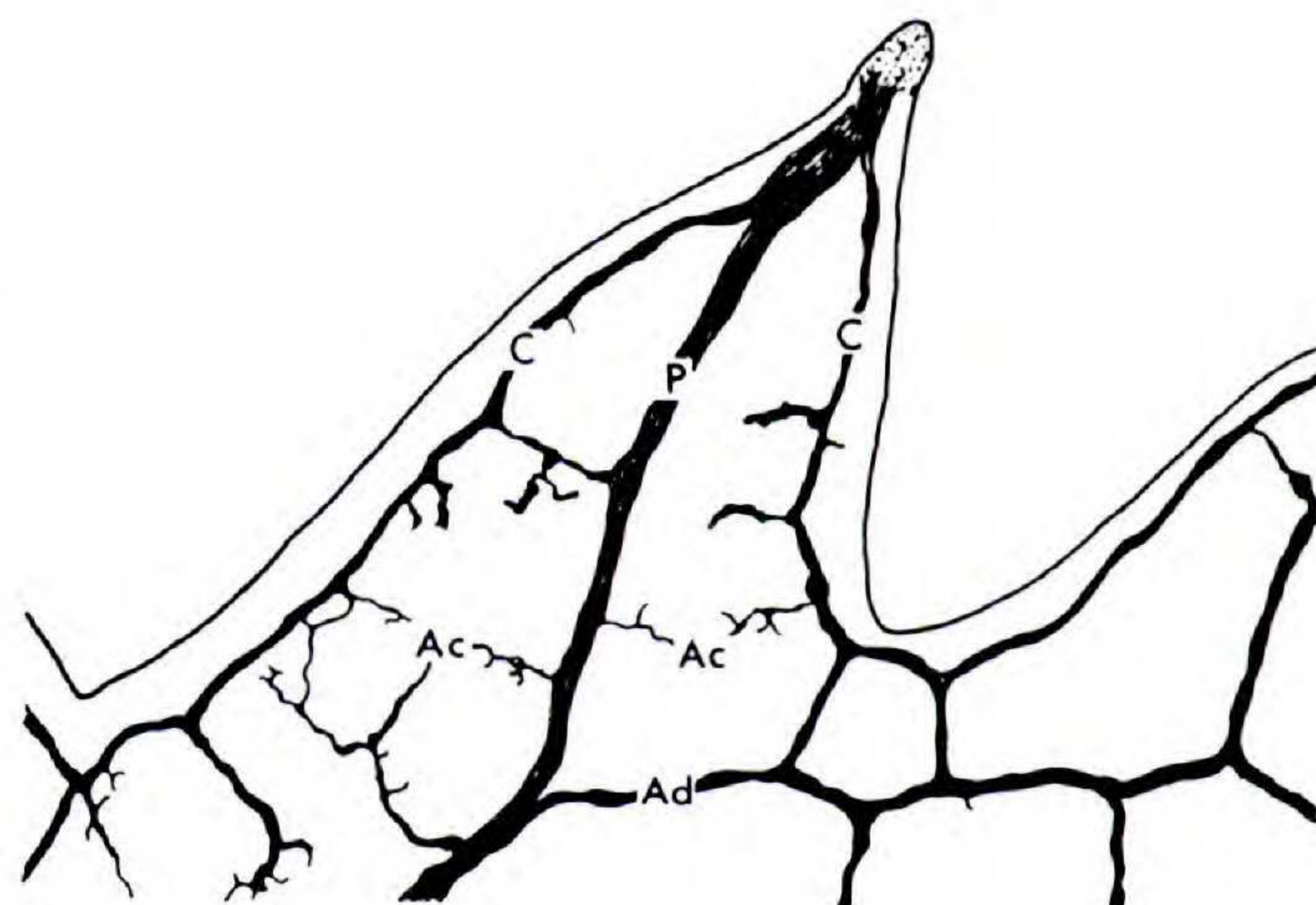


FIGURE 2. An ideal tooth with the major types of venation labeled. Ac—accessory veins, Ad—admedial vein, C—conjunctal veins, P—principal vein.

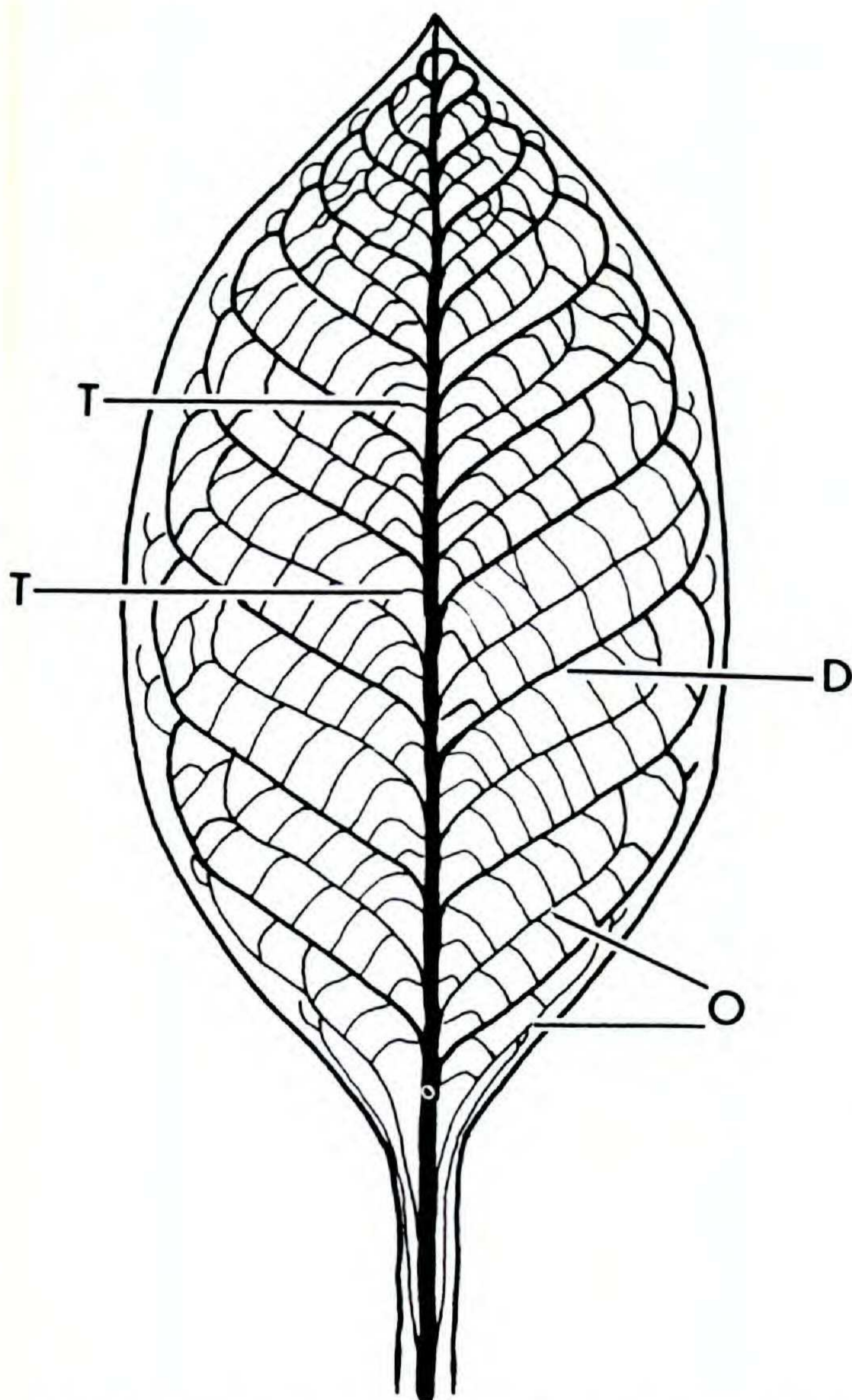


FIGURE 3. Venation of a simple leaf showing the deuterai (D), opadial (O), and trinal (T) veins.

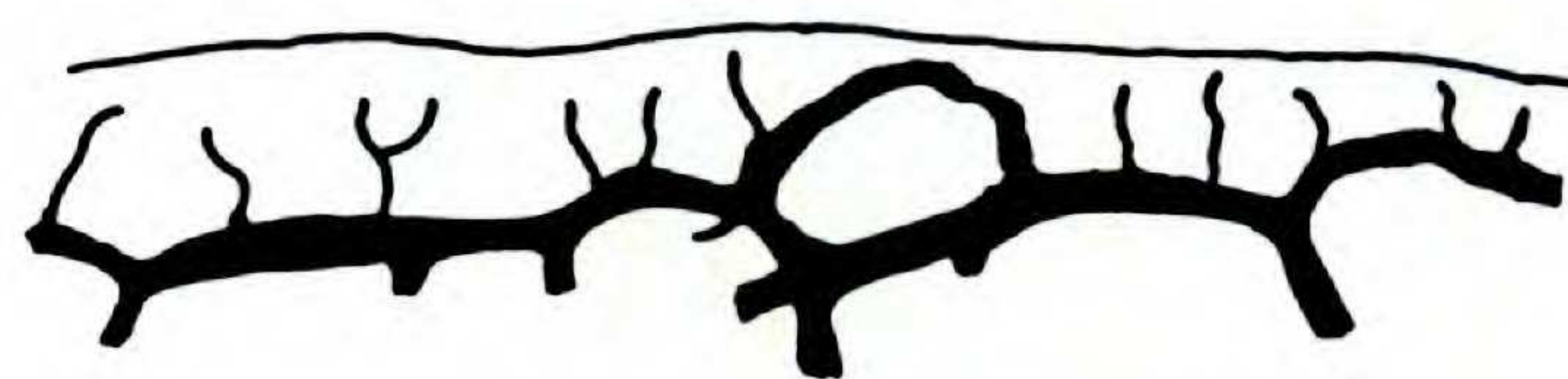


FIGURE 4. Spiked marginal ultimate venation.

#### LEAF ARCHITECTURAL DESCRIPTION OF *TICODENDRON INCOGNITUM*

Leaves alternate with encircling bases, stipulate with deciduous stipules attached to a ridge of petiolar tissue that extends transversely from the sides of the enlarged and raised site of leaf attachment (Fig. 7). Stipules completely encircling the apical and axillary buds. Leaf abscission scars with three traces, lacunae 3. Leaf simple, symmetrical, except slightly asymmetrical at the base; shape elliptical with a length to width (l/w) ratio of from 1.8 to 2.8 (mean 2.1, standard deviation 0.2, N = 15). Apex attenuate, base acute, texture chartaceous (Fig. 5).

The leaf margin is serrate in a single order with from 5 to 12 teeth (mean = 11) per side; generally there is one tooth per secondary vein with an average spacing in mature leaves of 1.3 cm. Serrations concave on their apical and basal sides (type C3) and have elongate, abaxially directed, soon deciduous, glandular tylate processes (a capitate pad of clear glandular tissue at the tooth apex; Fig. 8). The principal vein of the serration is medial and represents the continuation of a secondary vein that enters the serration straight and is then deflected slightly downward (Fig. 5). Principal vein termination tapered to abrupt, the principal accompanied by an admedial vein and at least one admedial conjunctal vein with accessory branches on its inner margin (Fig. 18). Conjunctal veins in opposite pairs when both are present. The presence of a medial principal vein and conjunctals on both sides of the principal in a tooth of this morphology implies that *Ticodendron* possesses modified rosoid teeth in the classification of Hickey & Wolfe (1975). The sinuses between the teeth are rounded and unbraced but are approached by a conjunctal vein or a branch from the conjunctal.

Venation pinnate, craspedodromous (Fig. 5). Secondaries diverge at a moderate acute angle (45–60°) and have a uniform spacing and angle of divergence. Secondaries slightly recurved and unbranched until they reach the base of the serration where they give off a comb vein, that is, a branch that runs close to the margin while giving off several tertiary veins to the superadjacent secondary (see

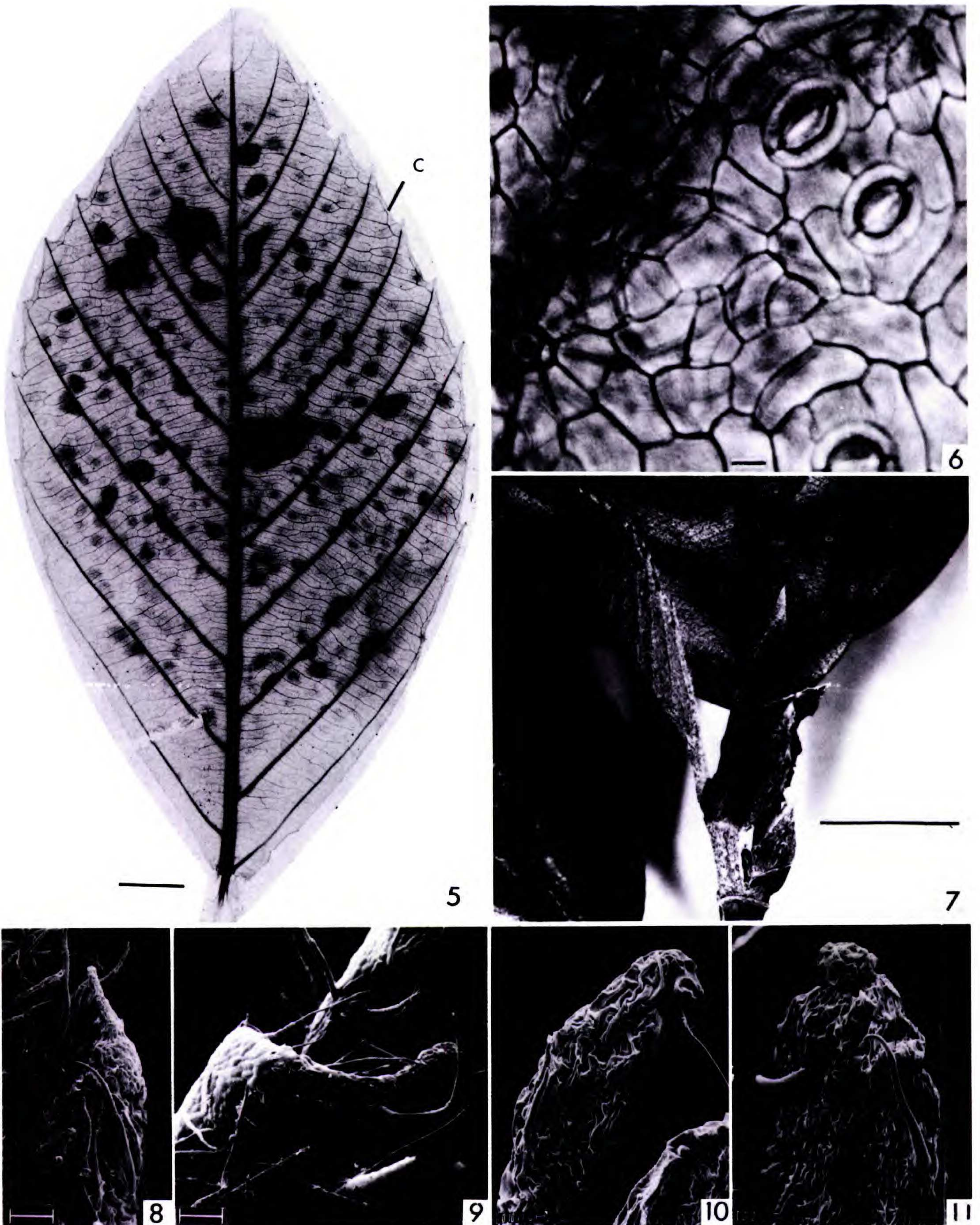
same size-class or whose size is part of a smooth gradation of sizes and whose behavior does not differ markedly from the majority of secondaries (Fig. 3, D).

(8) *opadial veins*—comprising the intersecondaries and those secondaries of abruptly different size and behavior from the majority of the secondaries (Fig. 3, O).

(9) *trinal veins*—the next thinnest vein set consisting of those tertiary veins that connect to the midrib and which arise either from secondary veins or from intersecondaries (Fig. 3, T). The sum of these three vein sets will be designated as the D-O-T veins collectively.

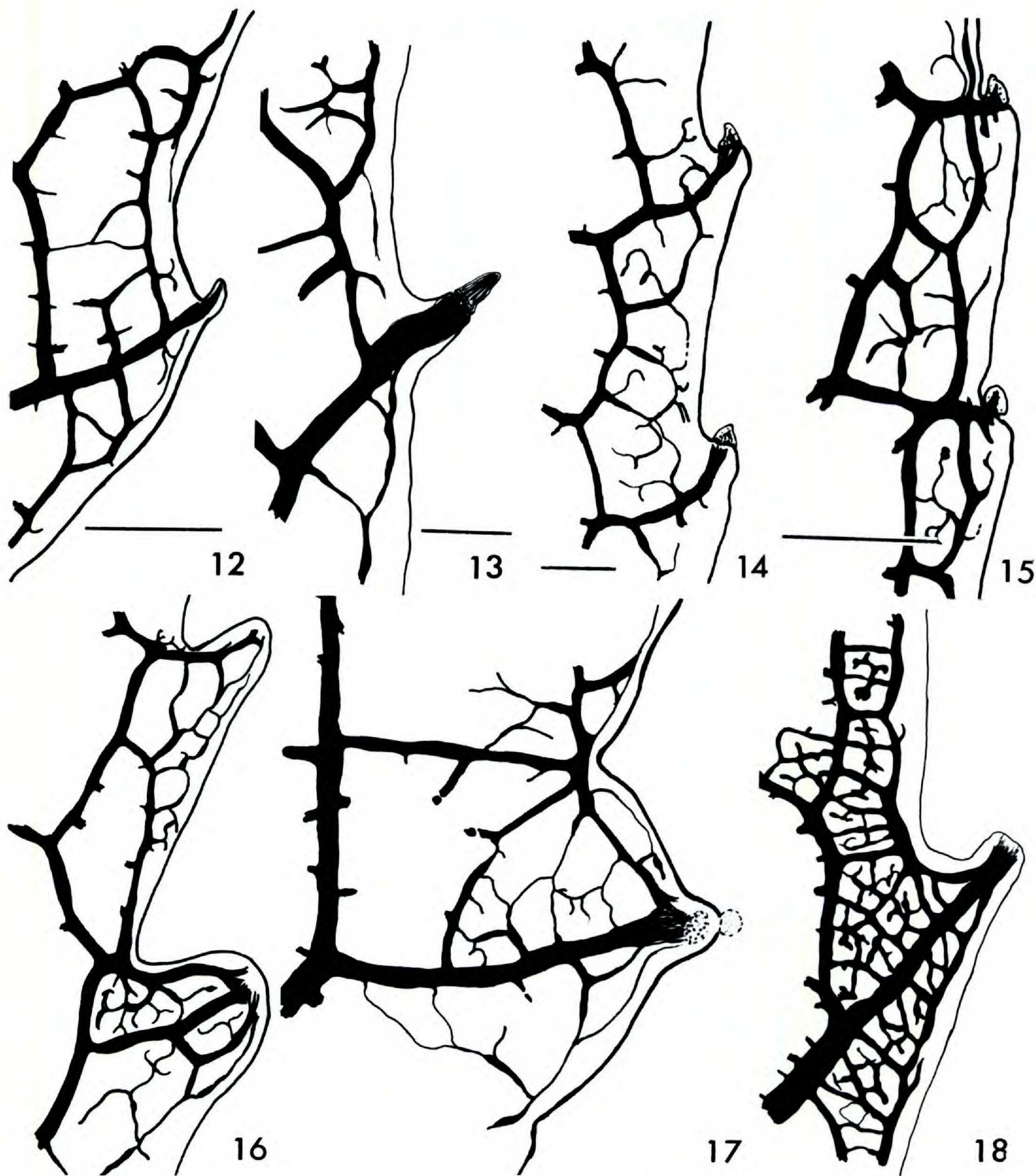
A final addition to the original set of leaf architectural terms involves a new term for the configuration of the marginal ultimate venation, as follows:

(10) *spiked*—margin with short, outward-pointing ultimate veins that are either unbranched or with a single pair of short branches (Fig. 4).



FIGURES 5-11. Details of leaf characters. 5-8. *Ticodendron incognitum* (Hammel et al. 15285, YU).—5. Whole cleared leaf. c—comb vein (NCLC 6383). Scale bar = 10 mm.—6. Lower cuticle showing hair base and stomatal anomocytic complexes (NCLC 6383). Scale bar = 100  $\mu$ m (0.1 mm).—7. Apical portion of woody twig. Note the large stipules that encircle the axes, and in the node below, the circular scar that remains on the axis. Scale bar = 10 mm.—8. Scanning electron microscope (SEM) view of a tooth of an unexpanded leaf; note the elongate process at its apex. Scale bar = 100  $\mu$ m (0.1 mm).—9. *Davidsonia puriens*, tooth of a young leaf with an elongate, slightly bulbous process near its apex (Cronquist 11622, NY). Scale bar = 100  $\mu$ m (0.1 mm).—10. *Castanea dentata*, young tooth with apical, capitate process (Nichols s.n., YU). Scale bar = 10  $\mu$ m (0.01 mm).—11. *Corylus americana*, young tooth with a short, apical, deciduous process (Nichols s.n., YU). Scale bar = 10  $\mu$ m (0.01 mm).





FIGURES 12-18. Camera lucida drawings of teeth from cleared leaves.—12. A typical dillenioid tooth from *Doliocarpus dentatus* (Dilleniaceae) (Bartlett 11367, US) (NCLC 857).—13. A tooth of *Tetracera volubilis* (Dilleniaceae) with the typical dillenioid-type architecture but with a deciduous process (Gentle 3363, US) (NCLC 828).—14. A typical theoid tooth from *Hartia sinensis* (239672, US) (NCLC 5).—15. Tooth of *Ceratopetalum gummiferum* (Cunoniaceae), which has many similarities to the theoid tooth in 14 (Wilkes s.n., YU) (NCLC 6713).—16. Two dimorphic teeth of *Canacomyrica monticola* (Myricaceae). The upper tooth is a typical cunonioid tooth while the lower is a rosoid tooth. Note the asymmetrical venation in the lower tooth (Hickey 5210, YU) (NCLC 5210).—17. A typical rosoid tooth from *Alnus nepalensis*. Note the asymmetrical venation in the tooth and the sometimes deciduous apical tip (Stibolt s.n., US) (NCLC 5387).—18. A tooth of *Ticodendron incognitum*. Note the similarities to the teeth in 16 and 17 indicating that it is a rosoid tooth (McPherson 8401, YU ex MO) (NCLC 6765). All scale bars 1 mm. Figure 16 same magnification as 14, 17 same as 15, and 18 same as 13.

TABLE 4. Table of the similarity of *Ticodendron* to other OTUs in each data set. These figures are calculated from the number of shared characters divided by the number of characters known for each OTU. OTUs are identified in Table 1.

	Data set 1	Data set 2		
	(leaf characters)	a (all characters)	b (leaf characters)	c (reproductive & wood)
FAGO	0.537	0.491	0.537	0.500
BRUN	0.500	0.373	0.500	0.095
ACSM	0.319	0.304	0.319	0.273
CERA	0.250	0.243	0.250	0.227
CUNO	0.277	0.304	0.277	0.364
DAVI	0.312	0.290	0.312	0.238
PTER	0.312	0.371	0.312	0.500
PLAT	0.333	0.400	0.333	0.545
RHOI	0.417	0.471	0.417	0.590
CANA	0.250	NA	NA	NA
MYRI	0.354	0.429	0.354	0.591
CAOP	0.521	NA	NA	NA
CAST	0.458	0.377	0.458	0.190
NOH1	0.354	0.426	0.354	0.600
NOH2	0.458	NA	NA	NA
ALN1	0.375	0.478	0.375	0.714
ALN2	0.458	NA	NA	NA

C on Fig. 5). Secondaries in 5–11 pairs; intersecondary veins lacking.

Tertiary veins percurrent, opposite, closely spaced ( $> 0.5$  mm); sigmoidally curved; exmedial angle of origin slightly acute to perpendicular (mean  $85^\circ$ , mode  $90^\circ$ ); admedial angle displaying the highly unusual character of being markedly obtuse (mean  $95^\circ$ , mode  $97^\circ$ ). Fourth-order veins strongly impressed, orthogonal; fifth order strongly impressed, generally random; highest vein order fifth; marginal ultimate venation looped. Freely ending veinlets present, curved, mostly twice-branched. Areolation well developed, randomly oriented, mostly quadrangular, of medium size (mean diameter 0.6 mm); leaf rank (following Hickey, 1977)  $3r^1$ .

Upper epidermis with straight-sided cells and many radial arrays of cells as from a hair base. Lower epidermis with anomocytic (rarely approaching cyclocytic) stomates, guard cells with thickened polar walls and a highly distinctive annular thickening on their inner ledges (Fig. 6). Both epidermal surfaces, but most commonly the lower one, with what appear to be overthrust glands in pits formed by the projecting edges of the surrounding cells, which are sometimes aligned in radial arrays away from the pit. Trichomes very rare

in the mature leaf, common in immature specimens (Fig. 8); T-shaped, no scales noted.

#### GROSS PHENETIC AND PHYLOGENETIC AFFINITIES

The similarity of the leaves of *Ticodendron* to our OTUs is given in Table 4. The combination of simple, craspedodromous leaves with a single tooth per secondary, angle of basal secondary origin the same as for the upper secondaries, an excess of 60 D-O-T veins; strongly percurrent, sinuous tertiary veins; with teeth having a tapered or abrupt, but not bulbous, termination; one or sometimes two pairs of conjunctal veins with inward-branching accessories; and the presence of marginal comb veins strongly suggests a group of taxa in the so-called Amentiferae, consisting of the Fagaceae including *Nothofagus*, Betulaceae, the fossil genus *Fagopsis*, and also the family Brunelliaceae (Rosales). In addition, the venation and marginal configuration of some pinnately compound leaves in the Juglandaceae and the Rhoipteleaceae warranted a more careful comparison to those families. Emphasis on the amentiferous group of genera is reinforced as well by the reduced flowers (Tobe, 1991) and the pollen (Feuer, 1991) found in *Ticodendron*.

Leaves of the extinct genus *Fagopsis*, with a similarity coefficient of 0.537 (Table 4), are most like those of *Ticodendron* even to the tapered terminal portion of the principal veins of its teeth. However, *Fagopsis* has convex-convex teeth (character 4) lacking conjunctal veins (16), angular sinuses (5), uniformly symmetrical leaf bases (47), well-developed areolation (31), and a deuterol-opadial-trinal (D-O-T) vein total of between 41 and 60 (35) as opposed to  $> 60$  for *Ticodendron*.

Among living genera, *Brunellia*, *Castanopsis*, and *Castanea* have similarity coefficients ( $s$ ) of 0.50, 0.521, and 0.458, respectively, and also share the character of having tapered terminations of the principal veins of their teeth. Furthermore, both *Castanea* and *Castanopsis* have rounded sinuses similar to those of *Ticodendron*. However, *Brunellia* has pinnately compound leaves (character 1) with angular sinuses and semicraspedodromous secondaries (29), while the two fagaceous genera have teeth with tylate processes (22), non-deciduous stipules (25) that are not attached to the expanded leaf base (26), more than 18 deuterol veins (33), and a total of deuterol and opadial veins that ranges between 18 and 28 (34). All three genera have well-developed areoles (31) and glandular peltate and simple trichomes (36).

Leaves of *Alnus* ( $s = 0.458$  and  $0.375$ ) and

*Nothofagus* ( $s = 0.458$  and  $0.354$ ) are similar to those of *Ticodendron* in their general shape and vein configuration. However, both genera lack the comb veins (character 44) found in *Ticodendron*, and most other genera of Rosidae examined have well-developed areoles (31), glandular peltate trichomes (*Nothofagus*) or both glandular peltate and simple ones (*Alnus*) (36), D-O-T vein numbers of between 41 and 60 (35), and splayed (*Alnus*) (Fig. 17) or truncate and splayed (*Nothofagus*) terminations to the principal veins of the teeth (18). *Alnus* differs further from *Ticodendron* in having two orders of convex-convex marginal teeth (4) with clear glandular (21), tylate (22) apices and splayed principal vein terminations (18) (Fig. 17). Additional differences between *Nothofagus* and *Ticodendron* include teeth of different shape (4), leaf bases that are always symmetrical (47), basal secondaries at a lower angle than those above (3), and petioles that have both wings and stipules attached (24) (see Tables 2, 3).

Among the remaining hamamelid genera examined in this study *Rhoiptelea* ( $s = 0.417$ ), *Platycarya* ( $s = 0.333$ ), and *Pterocarya* ( $s = 0.312$ ) were dissimilar because of their pinnately compound leaves. Two genera of the Myricaceae, *Myrica* ( $s = 0.354$ ) and *Canacomyrica* ( $s = 0.250$ ), have simple leaves but these show numerous differences such as teeth of the wrong shape (character 4) (Fig. 16), angular rather than rounded sinuses (5), a lack of stipules (24), symmetrical leaf bases (47), glandular, peltate, and simple trichomes (36), and a D-O-T vein number of from 19 to 38 (34).

These data suggest that the affinities of *Ticodendron* are with amentiferous families with rosid teeth (Hickey & Wolfe, 1975) which, despite their inclusion in the subclass Hamamelidae in the classifications of both Takhtajan (1969) and Cronquist (1988), have leaf architecture that is indistinguishable from that of the subclass Rosidae (Hickey & Wolfe, 1975; Wolfe, 1989). These two groups also share other characters (Dickison, 1989). For these reasons we also examined several other families of Rosales that are regarded as representing the most primitive families in Rosidae.

*Acsmithia* ( $s = 0.319$ ) is notable because it is the member of the Cunoniaceae with the highest level of similarity to *Ticodendron*. The genus has simple leaves with a single order of teeth (character 3) of the proper shape (4) and only of the rosid type. However, these teeth appear to be a less derived form of the rosid type than in *Ticodendron* because they possess a full set of accessory veins (8) and have splayed terminations. Other differ-

ences include opposite leaves (2) with semicraspedodromous venation (24) and paracytic stomates (37).

The above families form the basis of our cladistic analysis described below. In this, we used Cunoniaceae to polarize our characters. In Takhtajan's 1969 and 1980 classifications this family is thought to be the most primitive of his Saxifragales, the primitive order of Rosidae. Studies by Dickison (1975a, b, 1980a, b, 1984, 1989) have further strengthened the position of the Cunoniaceae. Cronquist (1988) also regarded the family as very primitive in the Rosales, although not the most ancestral. What is apparent for this family, like so many other truly primitive taxa, is the high degree of morphological variability to be found within it as well as the somewhat capricious expression of this variability (Dickison, 1989). Thus the family has, in some cases, tricolporoidate pollen (Hideux & Ferguson, 1976), extremely primitive wood (Dickison, 1977), and low- to moderate-rank leaves. Extreme variation is apparent in characters including the perianth, which varies from present to nearly absent, ovary position from hypogynous to epigynous, the frequent occurrence of a nectariferous disk surrounding the carpels (Dickison, 1984), and the presence of both simple and compound leaves within the same genus, such as *Weinmannia*. Cunoniaceae are especially variable in their carpellary morphology, which ranges from follicles to capsules and even drupes. Superficially the family runs nearly the whole gamut of diverse fruit types seen in the Rosidae and the Amentiferae, even to configurations seen in *Liquidambar* (*Pancheria*), *Staphelia* (*Gillbeea*), and *Pterocarya* (*Ceratopetalum*) (Dickison, 1984).

In addition, a number of fused, bicarpellate follicles with two stigmas or stigmas that approach fusion into a single bifid structure and whose flowers have highly reduced perianth are found in the genus *Acsmithia* and in the satellite family Davidsoniaceae (Dickison, 1984; Cronquist, 1981).

Cronquist (1988) has commented on the difficulty of distinguishing the Cunoniaceae and other Rosales from Dilleniidae. We uncovered a striking instance of this transitional position when we found marginal teeth in the leaves of the Australian genera *Ceratopetalum* and *Aphanopetalum* that closely resembled the theoid type found in the moderately derived Dilleniidae (Fig. 15 and compare to 14). Thus, the transformation to the cunonioid tooth type found in the Rosales and the amentiferous taxa discussed here must occur within the Cunoniaceae because both occur there.

Nothing closely resembling the rosid tooth type

TABLE 5. Comparison between data sets and different options. The options are addition of sequence = closest (closest), addition of sequence = simple (simple), unordered in part (part), and unordered all (all). Data set 1 included characters 1–48 and 18 OTUs, and data set 2 included all or parts of characters 1–70 and 14 OTUs.

Data set options	Number of trees	Length of trees	Consistency index
Data set 1			
Closest part	2	260	0.527
Simple part	2	260	0.527
Closest all	1	249	0.550
Simple all	15	250	0.548
Data set 2			
All characters			
Closest part	3	305	0.587
Simple part	3	305	0.587
Closest all	1	295	0.607
Simple all	2	294	0.609
Characters 1–48			
Closest part	1	213	0.601
Simple part	1	213	0.601
Closest all	9	204	0.627
Simple all	9	204	0.627
Characters 49–70			
Closest part	3	75	0.680
Simple part	3	75	0.680
Closest all	3	74	0.689
Simple all	3	74	0.689

with its frayed termination of the principal vein and conjunctals with inner branches occurs anywhere in the subclass Dilleniidae. Several genera of the family Dilleniaceae, including *Dillenia* and *Doliocarpus*, resemble *Ticodendron* in form, secondary venation, and strongly percurrent tertiaries (Wolfe, 1989). Their teeth (Figs. 12, 13), in contrast to *Ticodendron*, have the slightly bulbous termination of their principal veins that characterizes the dillenioid tooth type (Hickey & Wolfe, 1975), and lack conjunctals with inner branches and the comb veins that characterize many members of Rosidae. For this reason our search was limited to the Rosidae and Amentiferae.

#### EVOLUTIONARY ANALYSIS

Our evolutionary analysis of the relationships of *Ticodendron* progressed through a number of methodological stages, roughly along the lines suggested by Eldredge (1979) and Neff (1986). The first and potentially most important of these stages was character analysis (Kaplan, 1984; Neff, 1986;

Stevens, 1987; Steele et al., 1988). At this stage features are described, characters and character states are defined, and useful characters are selected. This is followed by character polarization in which ancestral states and structural transition series are identified. These characters and their polarized states are then used in the next stage. For this we used pattern sequence analysis to identify the optimal branching patterns. The last stage is systematic analysis, which uses a variety of data to identify the evolutionary relationships of the taxa.

We paid particular attention to character analysis during this research. Such an analysis produced a matrix showing the distribution of character states that are hypothesized to be structurally homologous. During this stage we made no attempt to equate structural homologies with evolutionary homologies. We considered that if the same character state is found in different taxa it is fundamentally similar in structure. We feel that our explicit terminology and rigorously defined character states facilitated our recognition of structurally similar features. In the Appendix, these characters are defined by topological, anatomical, or morphological similarity, while the states are distinguished by more subtle differences.

When assigning polarities to character states we hypothesized the ancestral states and the transitions between them using outgroup comparison (Maddison et al., 1984). Because we consider *Ticodendron* to be a member of Rosidae, for the reasons given above, we chose as our outgroup the family Cunoniaceae, which we consider to be primitive in the subclass.

The occurrence of theoid-type teeth in some Cunoniaceae (Fig. 15) permitted us to form a secondary outgroup lying outside of the Rosidae. Theoid teeth are found in at least two clades, the thealean clade and the flacourtialean clade (Hickey & Wolfe, 1975), and at this time it is neither clear that the origin of this tooth type is monophyletic nor which of the above clades is more closely related to the Rosidae. Based on this equivocal placement, we chose the Dilleniaceae as our secondary outgroup because of its inferred sister group relationship to the Rosidae, as well as the thealean and flacourtialean clades. The dillenioid tooth type (Figs. 12, 13) is clearly ancestral to the theoid-type tooth (Hickey & Wolfe, 1975) (Figs. 14, 15) and provides an unequivocal secondary outgroup.

A hypothetical ancestor was then formed for polarizing the character states and to root the trees. This was necessary when using PAUP because the program uses one taxon when several outgroups

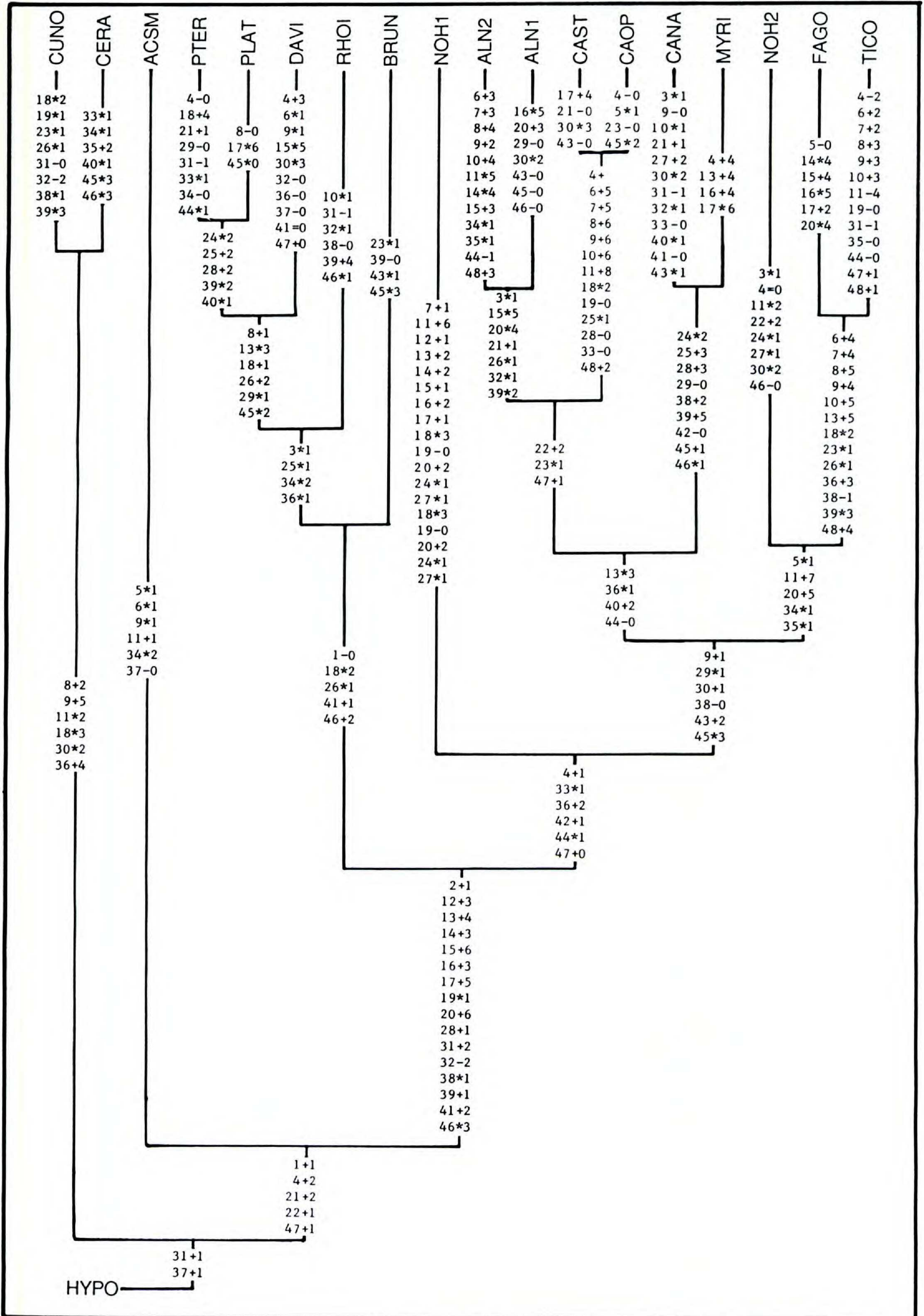
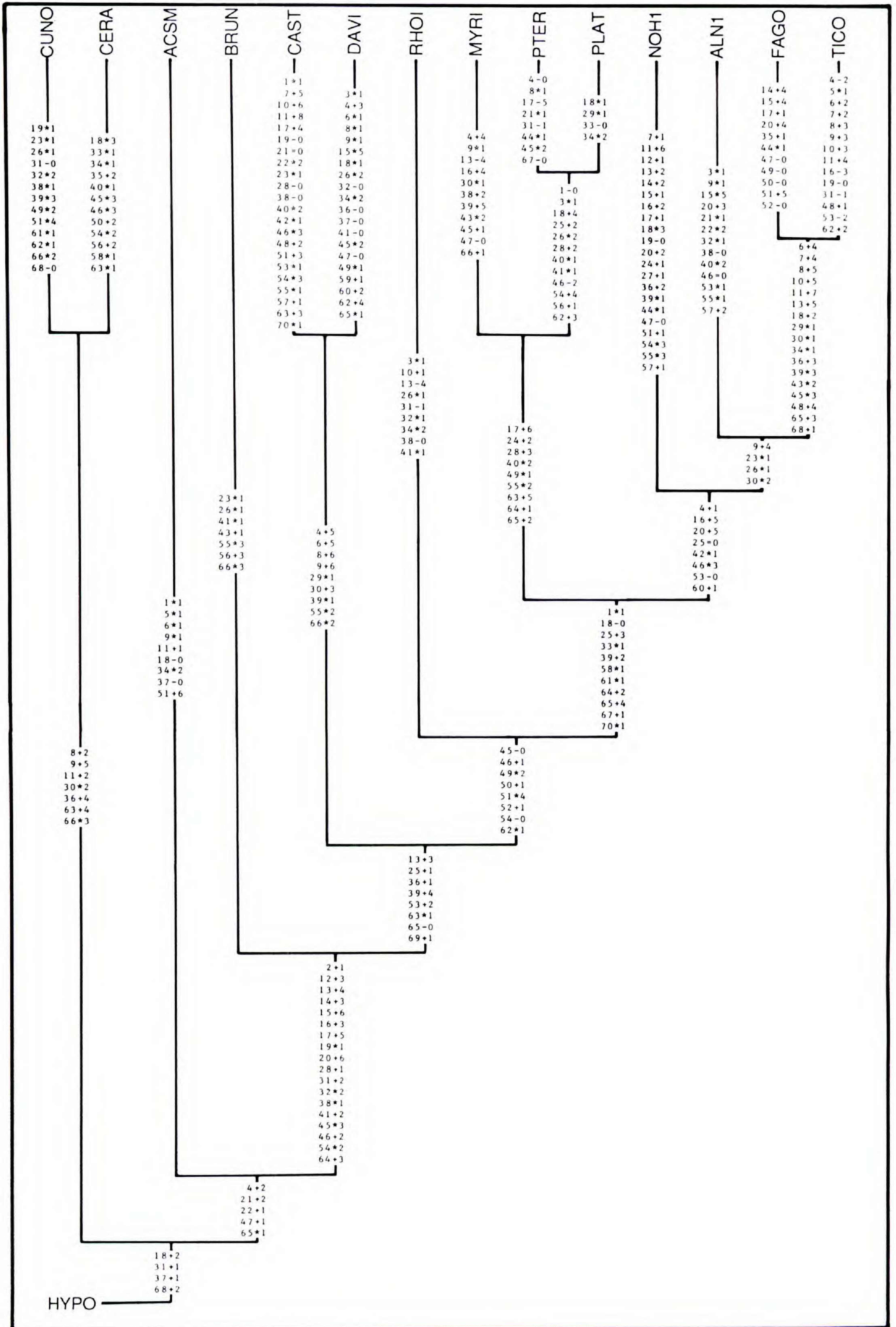


FIGURE 19. Cladogram of data set 1, which includes 48 leaf characters and 18 OTUs (Table 3). This is the shortest tree with 249 steps and a consistency index of 0.550. -, reversal; =, multiple reversal; \*, synapomorphy; +, parallelism.



are specified. Also, since there is no cladistic analysis of Cunoniaceae, the hypothetical ancestor had to be determined from the most common character states found in the three OTUs of Cunoniaceae. If states were equally common, the state shared with or found in the secondary outgroup was used. Some character states were ordered (see the Appendix). Those characters with only two states were ordered because we were able to specify by outgroup comparison which states were ancestral and which were derived. However, we polarized only a few characters with multiple states, based on structural transformations (see discussion of specific characters in the Appendix). All of our character polarizations are explicit hypotheses of the ancestral character states as well as the structural transformation in the characters that are ordered.

We performed a cladistic analysis as part of our pattern sequence analysis in order to identify the optimal branching pattern. PAUP uses parsimony to find trees with the minimum number of steps. Such an analysis gives hypotheses as to which structural homologies are evolutionarily homologous and which are evolutionarily homoplasous. In addition, it identifies the shared derived characters for each of the clades and taxa. Our analyses included two data sets, one with 48 leaf characters and 18 OTUs (Table 2) and a second that included 70 characters and 14 OTUs (Table 3). The latter data set was subdivided and resulted in three subsets: the first group has all the characters (designated as 2a), the second group (2b) has characters 1 to 48 (the same characters as data set 1) and the third (2c) has characters 49 through 70. Each analysis is summarized in Table 5 and discussed separately below.

The use of global branch swapping for data set 1 resulted in a single shortest tree (Fig. 19) of 249 steps and a consistency index of 0.550 (Table 5). The general topology of this tree has the cunonioid taxa *Ceratopetalum*, *Cunonia*, and *Acsmithia* at the base and a monophyletic origin for the remaining taxa, which are split into two clades. One clade includes the two juglandaceous taxa *Pterocarya* and *Platycarya*, and the OTUs *Davidsonia* and *Brunellia*. The second clade is essentially a fagalean clade with the addition of *Myrica* and *Canacomyrca* (Myricaceae). In this tree, *Ticoden-*

*dron* is the sister OTU to the fossil genus *Fagopsis*. The set of trees one step longer (Table 5) is similar to the shortest trees in their stability and variability of the topology. Thus it is significant that throughout both sets of trees, the relationships of the taxa of the Cunoniaceae never change, with *Acsmithia* remaining the sister group to the remaining taxa. In addition, these trees always had two clades, though in some trees *Brunellia* was placed as the sister OTU to both clades. Lastly, *Ticodendron* remained well-embedded in the fagoid clade but as a sister OTU to *Castanea* and *Castanopsis* or to *Fagopsis* and *Alnus*2.

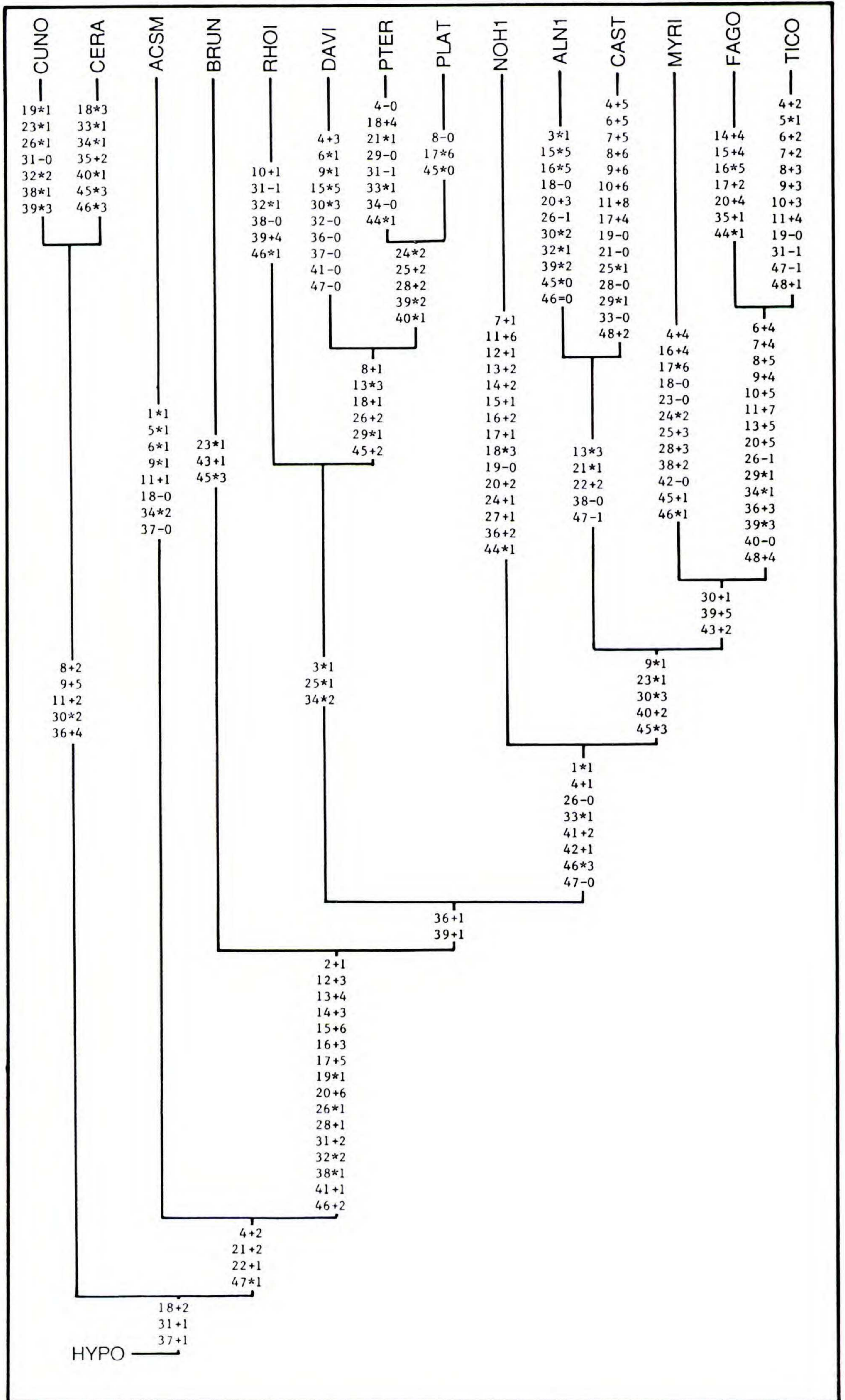
We have separated the synapomorphies into four categories based on the characters in our matrices and their distribution on the trees. The first are unistate synapomorphies, in which only one state exists in the entire clade above the node. The next are asymmetrical bistate synapomorphies, in which two states exist above the node, but one is considerably more common than the other. The third are asymmetrical tristate synapomorphies, which have three states above the node, with one much more common. The last are polystate synapomorphies, which have more than three states above the node or have additional states that are nearly as common.

Monophyly of the non-Cunoniaceae taxa is supported by 16 character states. Seven of these characters relate to the origin of what we term the type 2 (rosid) tooth but this tooth type is found in Cunoniaceae and other Rosidae, and it is not clear if its origin is monophyletic. Most of the synapomorphies for the clade are polystate. The exceptions include alternate leaf arrangement (character 2), which is a unistate synapomorphy; medial position of the principal vein in a type 2 tooth (12), an asymmetrical bistate synapomorphy; and stipule base that is wider than its attachment to the axis (28)—an asymmetrical tristate synapomorphy. The juglandoid clade is supported by six character states of which two are asymmetrical bistate synapomorphies. These are branching of the secondary veins common (46) and slightly zig-zag branching of the twigs (41). The fagoid clade is supported by six character states and all of the synapomorphies are polystate.

The analysis of data set 2a using global branch

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FIGURE 20. Cladogram of data set 2a, which includes 70 vegetative and reproductive characters and 14 OTUs. This is one of the two shortest trees with 294 steps and a consistency index of 0.609. The other shortest tree differs only by having *Davidsonia* as the sister OTU to all the higher taxa including *Castanea*, and *Castanea* becomes the sister taxon to the remaining OTUs. —, reversal; =, multiple reversal; \*, synapomorphy; +, parallelism.





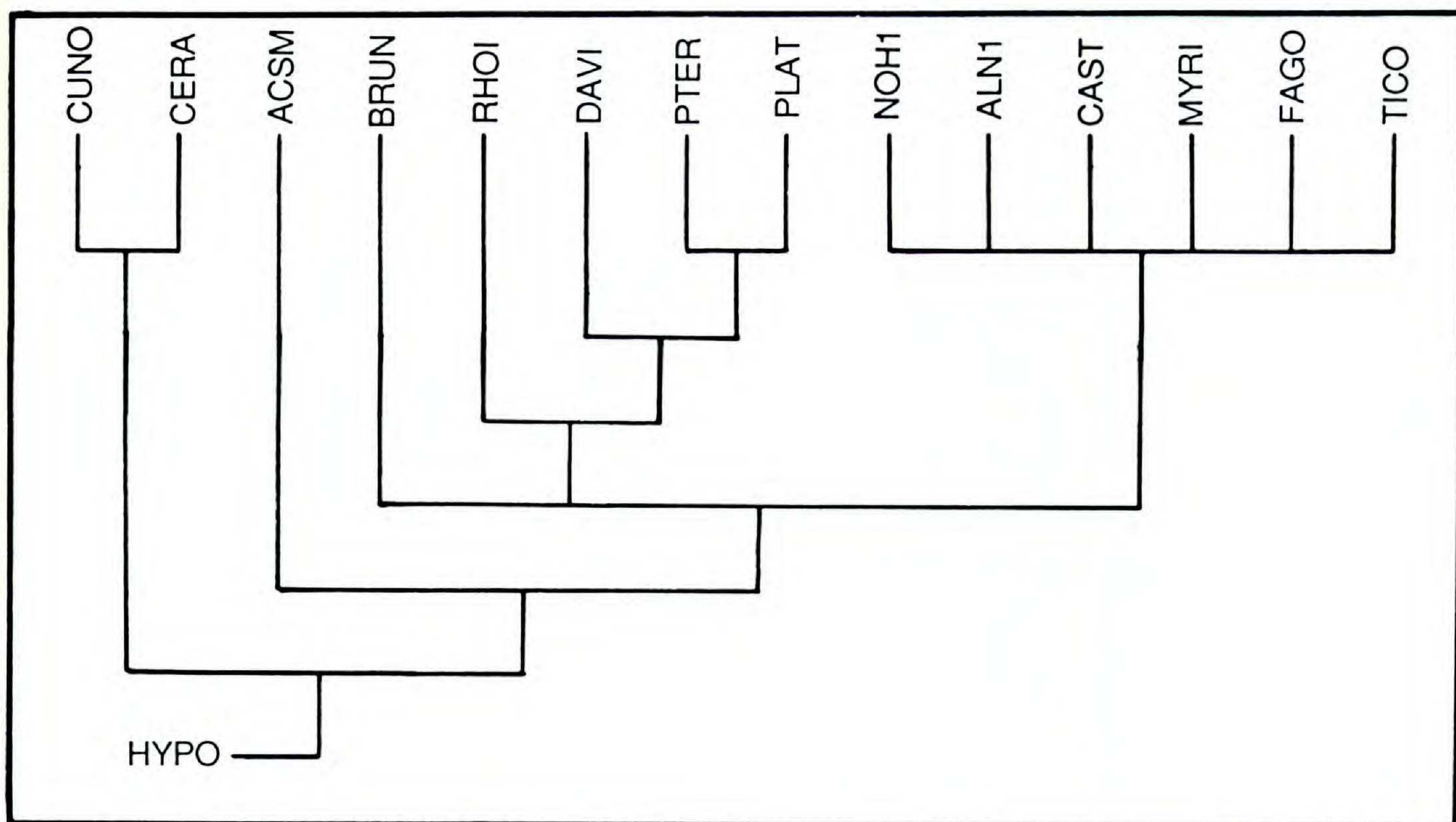


FIGURE 22. Strict consensus tree of the nine trees with the shortest length from data set 2b.

swapping (Fig. 20) resulted in two trees with 294 steps and a consistency index of 0.609 (Table 5). The general layout of the trees has the cunonioid taxa at the base and the remaining taxa forming a monophyletic group derived from *Acsmithia*. The other Rosales, *Brunellia* and *Davidsonia*, are at the base of this clade, followed by *Rhoiptelea* and the remaining hamamelid taxa, except that *Castanea* is placed as a sister group to *Davidsonia*. Again, *Ticodendron* is well-embedded at the top of the hamamelid clade near members of Fagales as a sister OTU to *Fagopsis*. This topology remains quite consistent in the other most parsimonious trees, with the only difference being that instead of having *Davidsonia* and *Castanea* as sister taxa, *Davidsonia* becomes the sister OTU to all the higher taxa including *Castanea*, which in turn becomes the sister taxon to the remaining members. The next most parsimonious tree, with one additional step, also has the same topology.

The monophyly of the taxa derived from the cunonioid *Acsmithia* is supported by 18 character states. Again, seven refer to character states of the rosid (type 2) tooth. A unistate synapomorphy is alternate leaf arrangement (character 2), while the medial position of the principal vein (12) in a

rosid tooth is a bistate synapomorphy. The presence of both admedial and accessory veins (14) is a tristate synapomorphy. Relationship of *Ticodendron* to the upper hamamelid clade is given by eight character states. A fused bract-bracteole complex (60) is a unistate synapomorphy, while an acuminate/acuminate (4) tooth shape is a bistate synapomorphy.

The cladistic analysis of data set 2b, performed with global branch swapping (Fig. 21), resulted in nine trees with a length of 204 steps and a consistency index of 0.627 (Table 5). The general topology of the tree has the OTUs of the Cunoniaceae at the base, and the remaining taxa forming a monophyletic group derived from *Acsmithia*. *Brunellia* appears next as a sister OTU to the remaining taxa that are again divided into two clades. One is the juglandoid clade with *Pterocarya*, *Platycarya*, and *Rhoiptelea*, while the second is the fagoid clade with the remaining taxa. *Ticodendron* is well-embedded in the fagoid clade and is the sister OTU to *Fagopsis*. A strict consensus tree of all nine most parsimonious trees (Fig. 22) shows the major differences from the tree described above (Fig. 21). Here the upper hamamelid clade is unresolved, as are the three clades leading to

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FIGURE 21. Cladogram of data set 2b, which includes 48 leaf characters and 14 OTUs. This is one of the nine shortest trees (consensus tree in Fig. 22) with 204 steps and a consistency index of 0.627. —, reversal; =, multiple reversal; \*, synapomorphy; +, parallelism.

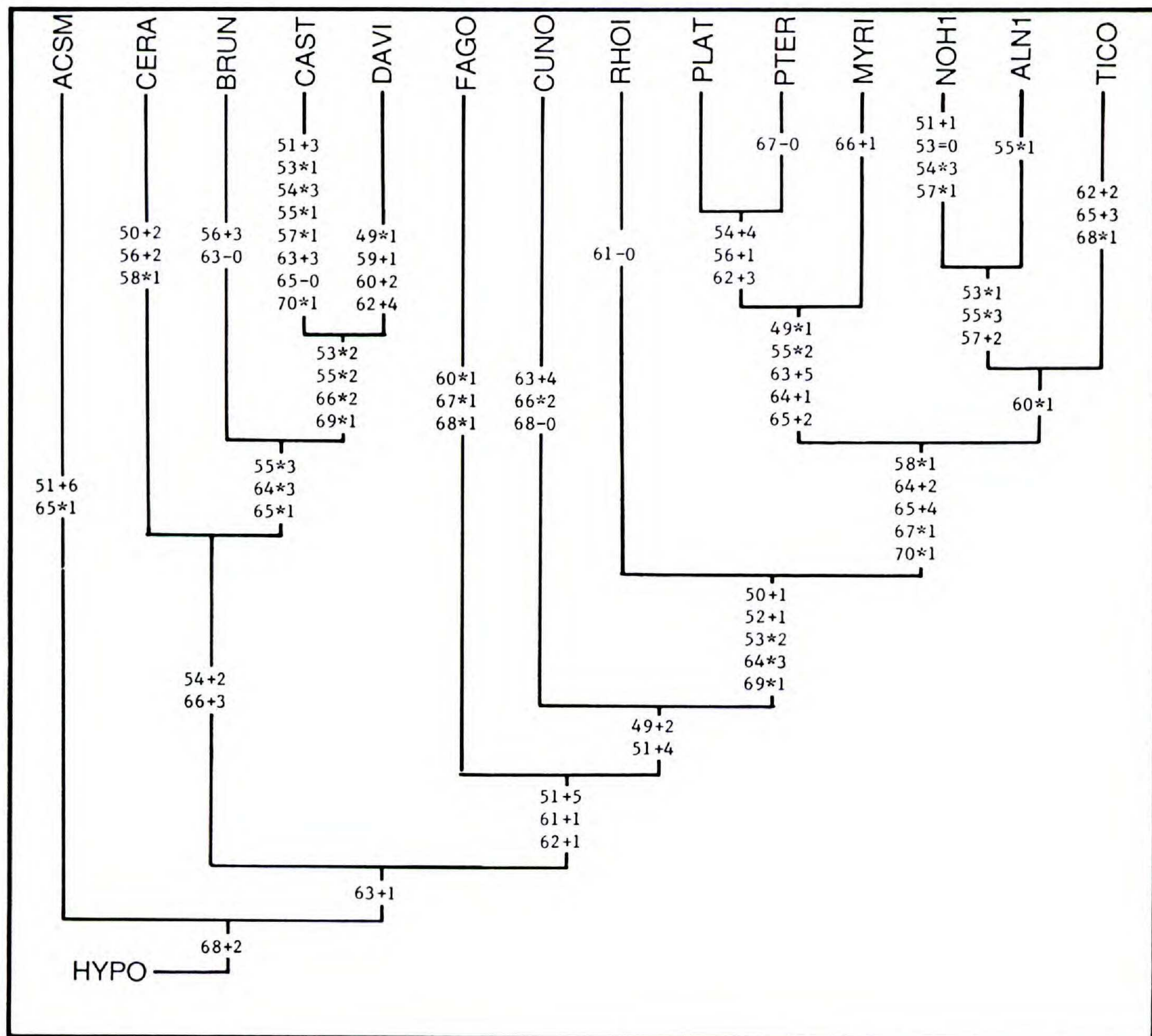


FIGURE 23. Cladogram of data set 2c, which includes 22 reproductive and wood characters and 14 OTUs. This is one of the three shortest trees (consensus tree in Fig. 24) with 74 steps and a consistency index of 0.689. —, reversal; =, multiple reversal; \*, synapomorphy; +, parallelism.

*Brunellia*, the Juglandaceae, and the upper hamamelids.

In data set 2b, the monophyly of the taxa derived from *Acsmithia* is supported by 16 character states of which seven refer to character states of the type 2 (rosid) tooth. The only unistate synapomorphy is alternate leaf arrangement (character 2), while the medial position of the principal vein (12) in a type 2 (rosid) tooth is a bistate synapomorphy. The presence of both admedial and accessory veins (14) is a tristate synapomorphy. The juglandoid clade is supported by three states while the fagoid clade is supported by eight states. The latter has one unistate synapomorphy—zig-zag twig branching (41)—and one bistate synapomorphy—axillary buds out of the plane of the leaf (42).

Our analysis of data set 2c, again using global branch swapping, produced three trees (Fig. 23)

that had a length of 74 steps and a consistency index of 0.689 (Table 5). The general topology has *Acsmithia* at the base with the remaining taxa forming a monophyletic group. This is split in turn into two groups, the first with *Davidsonia*, *Castanea*, *Brunellia*, and *Ceratopetalum*, and the second with the remaining taxa. Note that the second clade includes *Cunonia* (Cunoniaceae). *Ticodendron* is well-embedded in the second clade near some of the fagalean taxa. There are two other equally parsimonious trees. The only variation from this pattern is the relationships among *Ticodendron*, *Alnus*1, and *Nothofagus*1 as shown in the strict consensus tree (Fig. 24).

In this tree (Fig. 23) the monophyly of the taxa derived from *Acsmithia* is supported by a single polystate synapomorphy. The *Ceratopetalum*/*Brunellia* clade is supported by one bistate synapo-

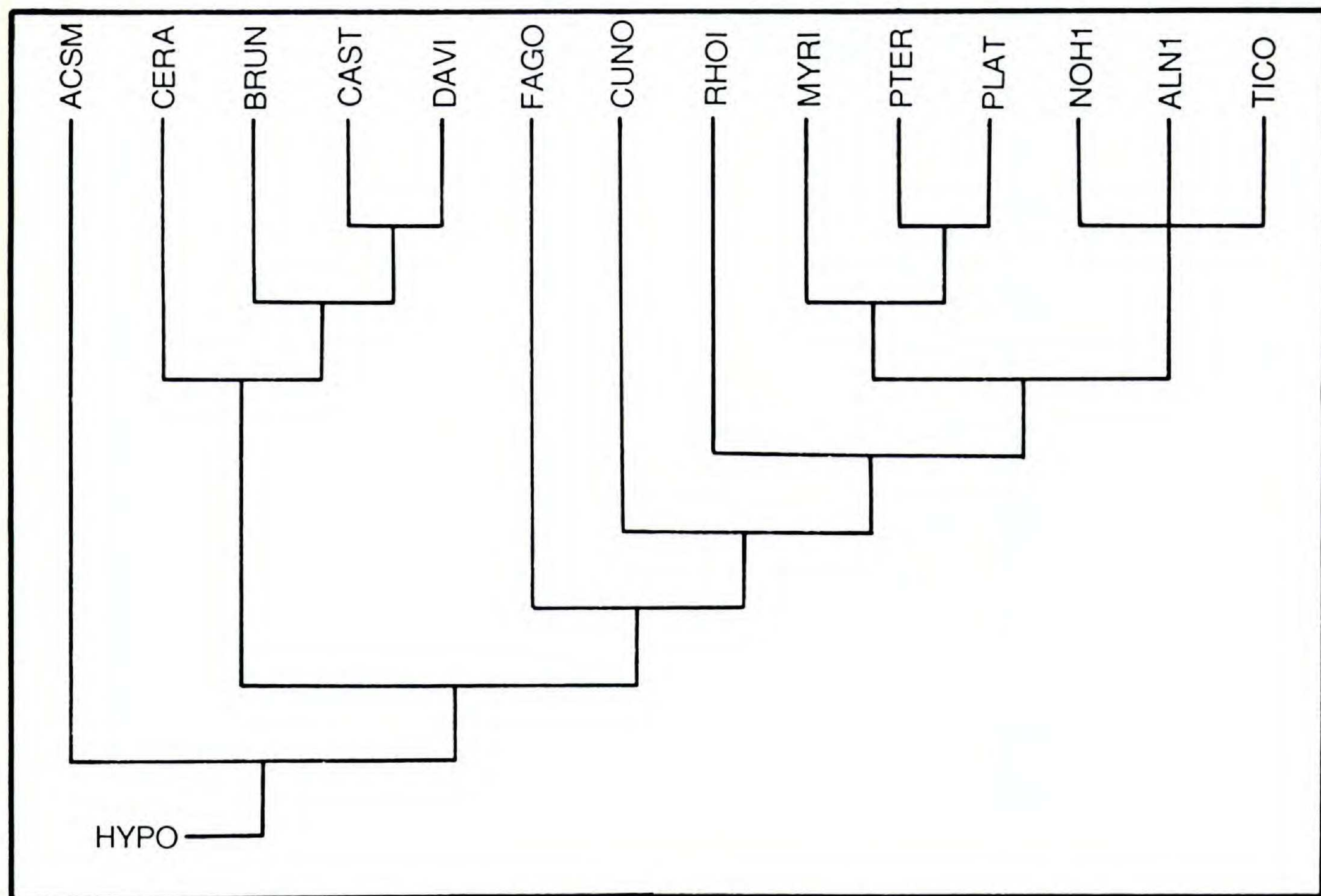


FIGURE 24. Strict consensus tree of the three trees with the shortest length from data set 2c.

morphy—vessels whose perforation plates are simple or scalariform with only a few bars (54). The second clade includes the remaining taxa and is supported by three characters of which two are unistate synapomorphies. These states include verrucate pollen sculpturing (51) and a simple, unbranched inflorescence (61).

In addition to these data sets we tried several experimental sets (Table 6). In these trials we attempted to use partially a priori methods to reduce the number of characters that were inappropriate for this hierarchy. We did this in order to resolve the situation that arises as the scope of a phylogenetic analysis is broadened to include more divergent groups, which causes certain characters to become homoplasous. Thus, in any randomly chosen set of characters, some characters will be more appropriate for comparisons at low hierarchical levels and some at higher. We thus devised a filtering method that was based on our two outgroups, Cunoniaceae and Dilleniaceae, to select characters appropriate to the hierarchy we examined. We suggest that if there is variability of characters between outgroups it may indicate a potentially homoplasous character for the ingroup. Our method was simply to remove any character that did not have any states shared in both outgroups.

In this way, 26 characters were removed, 25 from the leaf character set (1–48) and 1 from the list of other characters (49–70; Table 6). Although the topologies subsequently derived using these sets are generally similar to those found in the previous analyses, the cunonioid taxa switched position, with *Acsmithia* at the base and *Ceratopetalum* and *Cunonia* as sister taxa that together form the sister group to the remaining taxa. This is a particularly interesting result in light of previous suggestions that *Acsmithia* may be the most primitive genus in the Cunoniaceae (Dickison, 1989). The resulting tree lengths and consistency indexes are shown in Table 6. As one would expect, a smaller character base decreased the tree lengths and increased the consistency index; however, the resolution decreased because there were more trees of the same length. Note that, although the leaf data set (2b) had nearly the same number of characters as the nonleaf set (2c), the consistency index of the former was considerably higher. This suggests that these leaf characters may be better for resolving these relationships at the familial level among the so-called Amentiferae than the combination of reproductive and wood characters making up set 2c.

The sum of our cladistic analyses shows several general and recurrent similarities. *Ticodendron* is consistently placed with members of the Fagales

TABLE 6. Experimental data sets with characters removed. The characters in parentheses are the number of characters. The major options are addition of sequence = closest (closest), addition of sequence = simple (simple), unordered in part (part), and unordered all (all). Data set 1 included characters 1–48 and 18 OTUs, and data set 2 included all or parts of characters 1–70 and 14 OTUs.

Data set options	Number of trees	Length of trees	Consistency index
Data set 1 (23)			
Closest part	47	110	0.682
Simple part	47	110	0.682
Closest all	47	110	0.682
Simple all	47	110	0.682
Data set 2			
a All characters (54)			
Closest part	8	177	0.667
Simple part	8	177	0.667
Closest all	8	176	0.670
Simple all	8	176	0.670
b Characters 1–48 (23)			
Closest part	10	94	0.745
Simple part	10	94	0.745
Closest all	10	94	0.745
Simple all	10	94	0.745
c Characters 49–70 (21)			
Closest part	18	70	0.686
Simple part	18	70	0.686
Closest all	18	70	0.686
Simple all	18	70	0.686

and occasionally Myricaceae. The base of the clade is always found to lie with members of Cunoniaceae and other taxa considered to be members of the Rosidae by Takhtajan (1969, 1980) and Cronquist (1981, 1988). From our analyses it appears that Cunoniaceae may not be a monophyletic group, but we have not sampled the family sufficiently to show this. A major exception to the consistency of our analyses is the placement of *Fagopsis*, which switched from the top of the tree to near *Cunonia* near the base in data set 2c. This variability is probably due to the number of unknown character states in this fossil taxon.

Examination of the similarity matrices also shows comparable results (Table 4). *Ticodendron* is most similar to Fagales in data sets 1 and 2b, based on leaf data, though it is also similar to *Brunellia* and *Rhoiptelea*. The nonleaf data set (2c) also shows *Ticodendron* to be similar to Fagales and *Myrica* but with strong similarities as well to the two juglandaceous taxa and *Rhoiptelea*. Overall, *Ticoden-*

*dron* is similar to the two fagalean taxa *Fagopsis* (0.491) and *Alnus*1 (0.478), as well as to *Rhoiptelea* (0.471), *Myrica* (0.429), *Nothofagus*1 (0.426), and *Platycarya* (0.400) when all characters are included, as in data set 2a of Table 4.

Both the similarity matrices and the cladistic analyses show that the leaf and the nonleaf data sets have higher internal similarities or consistencies than does the combined data set. We suggest that this is partly due to the lack of evolutionary homology in some of the characters. In particular, the Normapolles-type pollen that is found in many members of Hamamelidae (e.g., *Pterocarya*, *Platycarya*, *Rhoiptelea*, *Myrica*, *Alnus*, and *Ticodendron*) and thought to be a natural group marked by synapomorphies (Muller, 1984), may actually have evolved more than once (Batten & Christopher, 1981; Batten, 1986; Kedves, 1989). Thus the pollen characters of this group may act to force these taxa together artificially. Another suite of characters that may have evolved independently is that of reduced flowers. Since reduced flowers of similar morphology are found in other nonrosid hamamelids (e.g., Urticales; Thorne, 1989), these are probably homoplasous characters.

Similarly, some leaf characters may be evolutionarily homoplasous at this familial level of analysis. These suspicions were confirmed when we ran experimental data sets in which about half of the characters were dropped, resulting in a dramatic increase in the consistency index. The fact that some of our leaf characters are evolutionarily homoplasous is not surprising at this early stage in the development of leaf architectural methods. As future studies refine the use of these characters our knowledge of their variability at various taxonomic levels will be established.

## CONCLUSIONS

Based on these analyses we suggest the following relationships. *Ticodendron* is most similar to an extinct taxon of Oligocene age known as *Fagopsis* (Manchester & Crane, 1983), and both of these taxa are most similar to members of the families Fagaceae and Betulaceae (in the sense of Cronquist, 1981). Manchester & Crane (1983) placed *Fagopsis* in the Fagaceae, but we do not feel that the structure of the female inflorescence or details of leaf architecture support assignment to that family. *Rhoiptelea* is a centrally placed taxon with relationships to both the juglandoid clade and the fagoid clade. *Davidsonia* is probably a sister taxon to Juglandaceae. Cunoniaceae is the sister group to all these taxa and has characters that are transitional to members of Dilleniidae as well. The

Cunoniaceae also appear to be paraphyletic but this needs further study.

From the standpoint of its systematic placement, therefore, our analysis demonstrates that the affinities of *Ticodendron* lie with the order Fagales (sensu Cronquist, 1981) but that it is clearly distinct from any of the families that are currently understood as belonging there. We therefore recommend that *Ticodendron* be recognized as a separate monotypic family of the Fagales. Although clearly closely related, the status of the fossil genus *Fagopsis* in relation to the new family is unclear because of a number of missing characters as well as the rather specialized nature of the fruiting structures in *Fagopsis*.

In addition to indicating the relationships of *Ticodendron*, this study demonstrates the utility of leaf characteristics. Comparisons of the consistency index of data sets 2b (leaf) and 2c (nonleaf) show very little difference. This indicates that these characteristics are as useful as floral, pollen morphological, and most anatomical characters that have traditionally been used in plant systematics. Interestingly, when we attempted to filter inappropriate characters from the experimental sets, we found that the consistency index of the leaf data set dramatically improved (Table 6). The leaf set had 23 characters and a consistency index of 0.745 while the nonleaf set had 21 characters and a consistency index of 0.686.

We believe that the best approach to such analyses is to select characteristics based on their information content at the appropriate hierarchical level. Our experimental data suggest that, for this level of the taxonomic hierarchy, the leaf data set probably includes more congruent characters than the set that includes characters from the highly reduced, largely wind-pollinated inflorescences of the Amentiferae (Thorne, 1989). Thus the leaf data set may actually be superior to the nonleaf set at this hierarchical level in this group of plants.

Finally, we feel that the analysis presented here has provided a plausible and consistent resolution for the surprisingly difficult systematic problems presented by this unusual new taxon. We also hope that this effort has shed some new light on the evolution of that group of rosid/hamamelid taxa loosely known as the Amentiferae and has elucidated some of the methods and characters whereby that analysis could be extended still further.

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APPENDIX. Characters and character states for the data matrices (Tables 2, 3) used to produce the cladograms in Figures 19-24, discussion of characters, and data on taxa that had more than one character state for each. The ancestral state based on outgroup comparison is 0; \* indicates that the character states are ordered; NA indicates not applicable.

1. \*Leaf organization: 0 pinnate compound, 1 simple.

True pinnate leaves, as opposed to ternately compound leaves, first appear in Rosales. Yet, in the primitive families, such as Brunelliaceae and Cunoniaceae, the leaf organization is not canalized, with both types found in the same genus and sometimes species. All leaves could be clearly assigned to one of the character states except for *Davidsonia*. This species is assigned the pinnately compound state, even though it is actually pinnatisect, with wings between the pinnae on the leaf axis.

2. \*Leaf arrangement: 0 opposite, 1 alternate.

Opposite leaves are not common in this group of OTUs nor in the primitive Dilleniidae or Rosidae. *Nothofagus* has a few species that are opposite.

Leaf margin:

3. \*Margin: 0 toothed in one order, 1 toothed in more than one order.

This character refers to a situation where there is a second order of teeth originating on the margins of the first. Two orders of teeth are widely distributed but not found in closely related clades.

4. Tooth shape (apical and basal margins): 0 concave, convex, 1 convex, convex, 2 concave, concave, 3 concave, acuminate, 4 acuminate, acuminate, 5 concave, straight.

The first term refers to the apical side and the second to the basal side of the tooth. There is considerable variation in tooth shape, which is dependent on basic tooth type, and specific derived modification of the types. *Canacomyrica* had both character state 1 and teeth that are convex, acuminate. In *Alnus* the small teeth are concave, concave.

5. \*Sinus shape: 0 angular, 1 smooth.

Angular sinuses are the most common type in angiosperms and in this group. *Castanea* and *Castanopsis* have both character states.

Tooth type 1: this type has the principal vein originating from close to the sinus and has no accessory vein along the admedial side.

This basic tooth type has previously been called cunonioid (Hickey & Wolfe, 1975) and our recent studies show that it is similar to the third tooth found in the

primitive Dilleniidae. All the ancestral character states are found in theoid teeth.

6. Position of principal vein of tooth type 1: 0 lateral toward apical sinus, 1 medial, 2 *Ticodendron* NA, 3 Betulaceae NA, 4 *Fagopsis* NA, 5 Fagaceae NA.

*Platycarya* most commonly medial (1) but also lateral (0).

7. Course of principal vein of tooth type 1: 0 apically deflected, 1 nothofagoid, principal displaced to sinus, 2 *Ticodendron* NA, 3 Betulaceae NA, 4 *Fagopsis* NA, 5 Fagaceae NA.

Some *Brunellia* are slightly basally deflected; *Acsmithia* are usually straight and only sometimes 0.

8. The presence of veins associated with the principal vein of tooth type 1: 0 both admedial and accessory, 1 only admedial, 2 only accessory, 3 *Ticodendron* NA, 4 Betulaceae NA, 5 *Fagopsis* NA, 6 Fagaceae NA.

In *Platycarya* the veins are usually missing and only sometimes are accessories found (2).

9. Strength of admedial vein of tooth type 1: 0 same vein order, 1 lower vein order, 2 Betulaceae NA, 3 *Ticodendron* NA, 4 *Fagopsis* NA, 5 Cunoniaceae NA, 6 Fagaceae NA.

10. Course of conjunctal veins close to tooth apex of tooth type 1: 0 none, 1 single, 2 in alternate pairs, 3 *Ticodendron* NA, 4 Betulaceae NA, 5 *Fagopsis* NA, 6 Fagaceae NA.

*Rhoiptelea* may be either none (0) or single (1).

11. Major vein(s) closest to sinus of tooth type 1: 0 admedial, 1 accessory or branch, 2 principal, 3 admedial and accessory, 4 *Ticodendron* NA, 5 Betulaceae NA, 6 nothofagoid: branch from principal, 7 *Fagopsis* NA, 8 Fagaceae NA.

Tooth type 2: this type has the principal vein originating medially and has at least a few teeth with an accessory vein along the admedial side.

The transitions between teeth in taxa with both types of teeth, transitions between taxa with only one type of tooth, and outgroup comparison suggest that type 2 teeth are derived from type 1. Note that in leaves with both types, type 2 teeth are associated with strong secondaries.

12. Position of principal vein of tooth type 2: 0 Cunoniaceae NA, 1 *Nothofagus* NA, 2 Brunelliaceae NA, 3 medial.

Although the teeth of the Magnoliidae and Dilleniaceae are medial, so are some type 1 teeth and theoid teeth.

13. Course of principal vein of tooth type 2: 0 Cunoniaceae NA, 1 Brunelliaceae NA, 2 *Nothofagus* NA, 3 straight, 4 apically deflected, 5 basally deflected.

The principal vein in *Fagopsis* is mostly straight (3) but occasionally basally deflected (5), and in *Platycarya* mostly straight (3) and sometimes apically deflected (4).

14. Presence of veins associated with principal vein of tooth type 2: 0 Cunoniaceae NA, 1 Brunelliaceae NA, 2 *Nothofagus* NA, 3 both admedial and accessory, 4 only accessory.

15. Strength of admedial vein of tooth type 2: 0 Cunonia-

ceae NA, 1 *Nothofagus* NA, 2 Brunelliaceae NA, 3 Betulaceae NA, 4 *Fagopsis* NA, 5 lower vein order, 6 same vein order.

16. Course of conjunctal veins of tooth type 2: 0 Cunoniaceae NA, 1 Brunelliaceae NA, 2 *Nothofagus* NA, 3 in opposite pairs, 4 in alternate pairs, 5 none.

*Ticodendron* mostly has only an admedial, but when there are conjunctals, they are in opposite pairs (3). *Myrica* has mostly alternate conjunctals (4) but occasionally opposite (3).

17. Fusion of principal and conjunctal veins of tooth type 2: 0 Cunoniaceae NA, 1 *Nothofagus* NA, 2 *Fagopsis* NA, 3 Brunelliaceae NA, 4 Fagaceae NA, 5 separate, 6 fused.

18. Termination of medial vein at apex of tooth: 0 splayed, 1 attenuate, 2 tapered, 3 truncated, 4 bulbous.

*Nothofagus* (2) has both splayed and bulbous terminations. *Brunellia* may be splayed (0) or tapered (2), *Canacomyrca* is tapered (2) but sometimes truncated (3), and *Myrica* is usually truncated (3) and less commonly splayed (0).

19. \*Sinus bracing of teeth: 0 not braced, 1 braced by convergent thickened veins.

Not braced (0) is the state found in most teeth of angiosperm leaves. *Brunellia* may be not braced (0) or braced (1).

20. Major vein(s) closest to sinus of tooth type 2: 0 Cunoniaceae NA, 1 Brunelliaceae NA, 2 *Nothofagus* NA, 3 admedial, 4 accessory or branch, 5 conjunctal or branch, 6 admedial and accessory.

*Nothofagus* usually has a branch from the admedial and rarely just the admedial (3).

21. Glandularity of tooth apex: 0 glandular, dark, 1 glandular, translucent, 2 nonglandular.

Glandular, dark apices (0) are found in the theoid tooth type; presumably homoplasous clear, glandular terminations are found in ancestral forms such as the Dilleniaceae. *Castanopsis* usually has character state 2 but occasionally has character state 0.

22. Apical morphology of teeth in cleared leaf preparations of mature leaves: 0 setaceous, 1 simple, 2 tylate.

Setaceous apices occur in theoid teeth and in presumed evolutionary transitions to that type.

*Castanopsis* is usually simple but sometimes tylate.

23. \*Characteristics of the leaf base or petiole: 0 does not encircle the axis, stipules discrete or missing, 1 encircles the axis (> 50% at apical nodes or if opposite, > 40%) and forms sheath or stipules.

Discrete stipules on the main axis apparently first appear in Rosales and the primitive, palmate Dilleniidae.

24. Presence of wings on the petiole or stipules associated with the base of the petiole: 0 has stipules, 1 has both wings and stipules, 2 no wings or stipules.

Wings are stipules associated with encircling leaf bases and are common in the Magnoliidae and primitive Dilleniidae.

25. Stipules deciduous below the second node with ex-

panded leaves: 0 yes, always deciduous, 1 no, not usually deciduous, 2 Juglandaceae NA, 3 Myricaceae NA.

Stipules generally appear deciduous in primitive groups. *Castanopsis* and *Castanea* both may have twigs that are deciduous (0) while others are nondeciduous (1).

26. Petiole attachment: 0 enlarged base without stipules attached, 1 enlarged base with portion of stipule attachment on base, 2 without enlarged base.

The distribution of this character is unclear. *Brunellia* and *Castanea* may be enlarged (1) or not enlarged (2).

27. Petiole scar: 0 3(4) trace/3 lacunar, 1 arc of more than 4 traces, 2 no scars visible.

*Castanopsis* and *Castanea* both have character states 0 and 1.

28. Stipule base: 0 not wider than attachment, 1 wider than attachment, 2 Juglandaceae NA, 3 Myricaceae NA.

Distribution of this character is unclear but from our observations it appears that stipules with narrow attachments (1) do not appear until the level of Flacourtiaceae and Cunoniaceae.

29. \*Principal venation: 0 pinnate semicraspedodromous, 1 craspedodromous.

Semicraspedodromous (0) is the general case in the primitive Dilleniidae and Rosidae. Craspedodromy is rare but found in the isolated clade originating in Dilleniaceae (e.g., *Doliocarpus*) and including Actinidiaceae. However, because of the difference in tooth type in their clade, the craspedodromous state here represents a homoplasy with the craspedodromous veins (1) of the Rosidae. *Davidsonia* usually has character state 1 but occasionally also 0, and *Myrica* is both brochidodromous and semicraspedodromous (0).

30. Angle of origin of lower basal veins: 0 with two pairs at a lower angle and subsequent at a higher angle though may be somewhat irregular in angle and spacing, 1 with basal no different in angle or spacing, 2 with basal pair at a lower angle and subsequent at a higher angle though may be somewhat irregular in angle and spacing, 3 basal vein at highest angle with subsequent veins at lower angles, 4 actinodromous.

Distribution of this character is variable, although it appears that those with two pairs at a lower angle (0) are more common in the primitive angiosperms.

31. Areoles: 0 incomplete, 1 imperfect, 2 well developed.

Incomplete areoles (0) are found throughout the primitive angiosperms and those with low-rank leaves.

32. Marginal venation: 0 incomplete, spiked, 1 incompletely looped, 2 looped.

Distribution of this character is unclear.

33. \*Number of deuterals: 0 greater than 18, 1 less than or equal to 18.

Distribution of this character is incompletely known, but in primitive angiosperm groups the number of deuterals is usually less than 10.

34. Number of deuterals + opadials: 0 19–28, 1 less than or equal to 18, 2 greater than 28.

Distribution of this character is incompletely known, but in primitive angiosperm groups the number of deu-

terals is usually less than 10, plus opadials is usually less than 15.

35. Number of deuterals + opadials + trinals: 0 greater than 60, 1 41–60, 2 less than or equal to 40.

Distribution of this character is incompletely known, but in ancestral angiosperm groups the D-O-T number is usually less than 35 in unreduced leaves.

36. Trichome type: 0 simple, 1 glandular/peltate and simple, 2 glandular/peltate, 3 T-shaped, 4 Cunoniaceae NA.

Distribution of this character is unclear.

37. \*Stomate type: 0 paracytic, 1 anomocytic, 2 variable.

Both paracytic (0) and anomocytic (1) stomates have a variable distribution in primitive angiosperms.

38. Dehision of tooth tip in young expanding leaf: 0 nondeciduous, 1 deciduous, 2 none.

Nondeciduous tooth apices are the general case among primitive angiosperms.

39. Shape of tooth tip in young expanding leaf: 0 short, stout, 1 elongate, capitate, 2 short, capitate, 3 elongate, simple, 4 *Rhoiptelea* NA, 5 *Myrica* NA.

Distribution of this character is unclear.

40. Direction of apex of tooth tip in young expanding leaf: 0 pointing abaxially, 1 pointing adaxially, 2 in plane of lamina.

Distribution of this character is unclear.

41. Branching of twigs: 0 straight, 1 slightly zig-zag, 2 zig-zag.

Distribution of this character is unclear.

*Castanopsis* and *Castanea* are zig-zag (2) to slightly zig-zag (1).

42. \*Axillary buds: 0 in plane of leaf base(s), 1 out of plane of leaf base(s).

Axillary buds in plane of leaf base (0) is the expected state for primitive angiosperms, but our observations of this character are incomplete.

43. \*Uniformity of course of basal secondaries compared to distal portion of leaf. 0 no, 1 nearly so, 2 yes.

Lack of uniformity in secondaries (0) is the general case in primitive angiosperms. Uniform, or nearly uniform (2, 1) secondaries have a similar distribution to character 29.

44. \*Existence of comb vein: 0 present, 1 absent.

Distribution of this character is unclear, although comb veins are often found in craspedodromous leaves.

45. \*The existence of intersecondaries: 0 common (greater than 40%), 1 few (3 to 5), 2 rare (1 or 2), 3 none (never any).

Intersecondaries are frequently found in the magnoliids and are lost in numerous groups of more derived dicots.

46. Branching of secondaries: 0 rare (1 or 2), 1 few (3 to 5), 2 common (greater than 40%), 3 none (never any).

Branched secondaries are common among the Magnoliidae.



47. \*Base of a number of leaves or terminal leaflets asymmetrical: 0 none (never any), 1 common.

Distribution of this character is unclear.

48. In type 1 teeth: 0 principal vein originates from near sinus, 1 *Ticodendron* NA, 2 Fagaceae NA, 3 Betulaceae NA, 4 *Fagopsis* NA.

49. Pollen shape: 0 prolate, spherical, 1 suboblate, spherical, 2 oblate.

The prolate to spherical shape (0) appears throughout the primitive triaperturate groups.

50. Pollen aperture: 0 colporate, 1 porate, 2 colpate.

The colpate condition appears throughout the primitive triaperturate groups, while the colporate condition (0) does not appear until the level of Flacourtiaceae and Cunoniaceae. The porate condition found in the Normapolles group probably had multiple origins. *Cunonia* is both colporate (0) and colpate (2).

51. Pollen sculpturing and density: 0 reticulate, 1 spinulose, moderate, 2 spinulose, few, 3 striate, 4 spinulose, many, 5 verrucate, 6 psilate/perforate.

Reticulate sculpturing (0) appears throughout the primitive triaperturate groups. *Cunonia* is both reticulate (0) and spinulose, many (4).

52. \*Exine type tectate/perforate: 0 columellate, 1 columellate-granular.

Columellae (0) appear throughout primitive angiosperms. The coding of Cunoniaceae is uncertain and needs TEM sections.

53. Exine proportions: 0 sexine greater than or equal to nexine, 1 sexine greater than nexine, 2 sexine much greater than nexine.

The distribution of this character is unclear. The coding of Cunoniaceae is uncertain and needs TEM sections.

54. Vessels: 0 scalariform with many bars, 1 scalariform with few bars, 2 simple and scalariform with moderate to many bars, 3 simple and scalariform with few bars, 4 simple.

Scalariform perforation plates with many bars (0) appear throughout primitive angiosperms.

55. Imperforate type: 0 tracheids and/or fiber-tracheids with good bordered pits, 1 tracheids and fibers with bordered pits, 2 fibers with bordered pits, 3 fibers without bordered pits.

The first state (0) appears throughout primitive angiosperms.

56. Axile parenchyma: 0 diffuse, 1 banded, 2 both, 3 other.

Distribution of this character is unclear. *Ceratopetalum* is banded (1) and sometimes diffuse (0).

57. Rays: 0 heterogeneous, 1-3+ seriate, 1 heterogeneous, 1-2 seriate, 2 homogeneous, 1-2 seriate.

The first state (0) appears throughout primitive angiosperms.

58. \*Ray crystals: 0 no, 1 yes.

Distribution of this character is unclear. The coding of *Acsmithia*, *Cunonia*, and *Pterocarya* for this character is not certain.

59. \*Bract-bracteole complex off main axes: 0 yes, 1 only bract, 2 no.

Distribution of this character is unclear. *Ticodendron* is variable, either 0 or 1, and dependent on the sex of the inflorescence. The coding of *Acsmithia* and *Cunonia* is not certain.

60. \*Bract-bracteole complex fused: 0 no, 1 yes, 2 Brunelliaceae NA.

The first state (0) appears throughout primitive angiosperms. *Ticodendron* is variable, either 0 or 1, and dependent on the sex of the inflorescence. The coding of *Acsmithia* and *Cunonia* is not certain.

61. \*Main inflorescence axis: 0 branched (panicle, cymose), 1 simple unbranched (unbranched catkin, thyrse, raceme).

The first state (0) appears throughout primitive angiosperms. *Cunonia* is probably variable between the two states.

62. Structure in axile of bracteoles: 0 inflorescence axis (complex cyme), 1 flower, 2 *Ticodendron* variable, dependent on sex of inflorescence, 3 nothing, 4 *Davidsonia* NA.

The first state (0) appears throughout primitive angiosperms. *Cunonia* has a variable inflorescence (0) and flower (1), and *Castanea* is mostly with an inflorescence (0) and occasionally a flower (1).

63. Gynoecium: 0 apocarpous, lateral-admedial, 1 2 syncarpous and ascidate, carpel and attachment lateral-admedial, 2 2 syncarpous and ascidate, carpel and attachment apical, 3 3 syncarpous ascidate, attachment lateral and admedial, 4 2 syncarpous ascoplicate, lateral admedial, 5 2 syncarpous and ascidate, carpel and attachment basal.

The apocarpous state of the gynoecium appears throughout primitive angiosperms. The syncarpous state has a variable occurrence and appears to have multiple origins. (Terminology and distribution from Taylor, in press).

64. Ovule integuments: 0 apobitegmic, 1 apounitegmic, 2 hemiunitegmic, 3 hemibitegmic.

The apobitegmic state (0) appears scattered throughout primitive angiosperms. (Terminology and distribution from Taylor, 1988, in press.) Coding of *Brunellia*, *Acsmithia*, *Cunonia*, *Davidsonia*, *Nothofagus*, and *Alnus* is not certain.

65. Ovule morphology: 0 bitegmic, hemianatropous, 1 bitegmic, anatropous, 2 unitegmic, orthotropous, 3 unitegmic, hemianatropous, 4 unitegmic, anatropous.

The bitegmic, hemianatropous state (0) is common throughout primitive angiosperms. (Terminology and distribution from Taylor, 1988.) Coding of *Acsmithia*, *Cunonia*, *Castanea*, *Nothofagus*, and *Alnus* is not certain.

66. Stamen attachment and tip: 0 basal with apical extension, 1 basal without apical extension, 2 dorsiventrally fixed without apical extension, 3 dorsiventrally fixed with apical extension.

The first state (0) appears throughout primitive angiosperms. *Rhoiptelea* is either 0 or 1, and coding of *Davidsonia* and *Platycarya* is uncertain.

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67. \*Flowers: 0 bisexual or reduced bisexual, 1 unisexual.

The first state (0) appears throughout primitive angiosperms.

68. Perianth other than bract-bracteoles: 0 yes, two whorls, 1 no, 2 yes, one whorl.

Distribution of this character is unclear. *Ceratopetalum* is variable with character state 0 or 2 and *Fagopsis* is uncertain. We consider the vascularized papillae in *Myrica* to be perianth.

69. \*Endosperm: 0 yes, 1 no or scanty.

The first state (0) appears throughout primitive angiosperms.

70. \*Ovary: 0 superior, 1 inferior or semi-inferior.

The first state (0) appears throughout primitive angiosperms. Cunoniaceae coding is uncertain, and see perianth for *Myrica* coding.